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A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

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With five plates

Sect. 11. Phyllanthus

Phyllanthus sect. Euphyllanthus sensu Muell. Arg. in DC. Prodr. 15(2): 374. 1866 (ex p.).

Annual or perennial herbs or subshrubs, with phyllanthoid branching; branchlets simple. Monoecious or dioecious, the flowers in unisexual cymules (the female then solitary) or (in a few species) in bisexual cymules. Male flower: calyx-lobes (4) 5 or 6; disk divided into segments isomerous with the calyx-lobes; stamens 2 or 3 (very rarely 4); filaments free or united into a column, anthers extrorse (except in *P. maestrensis*) and usually dehiscing horizontally or obliquely; pollen grains 3- or 4-colporate, the exine reticulate. Female flower: calyx-lobes 5 or 6, usually larger than the male, persisting in fruit; disk entire or variously lobed or dissected; ovary smooth, obscurely stipitate; styles usually free except at the very base, bifid, the tips of the branches thickened or more often slender. Capsule oblate, elastically dehiscent; columella persistent; seeds sharply trigonous, variously ornamented.

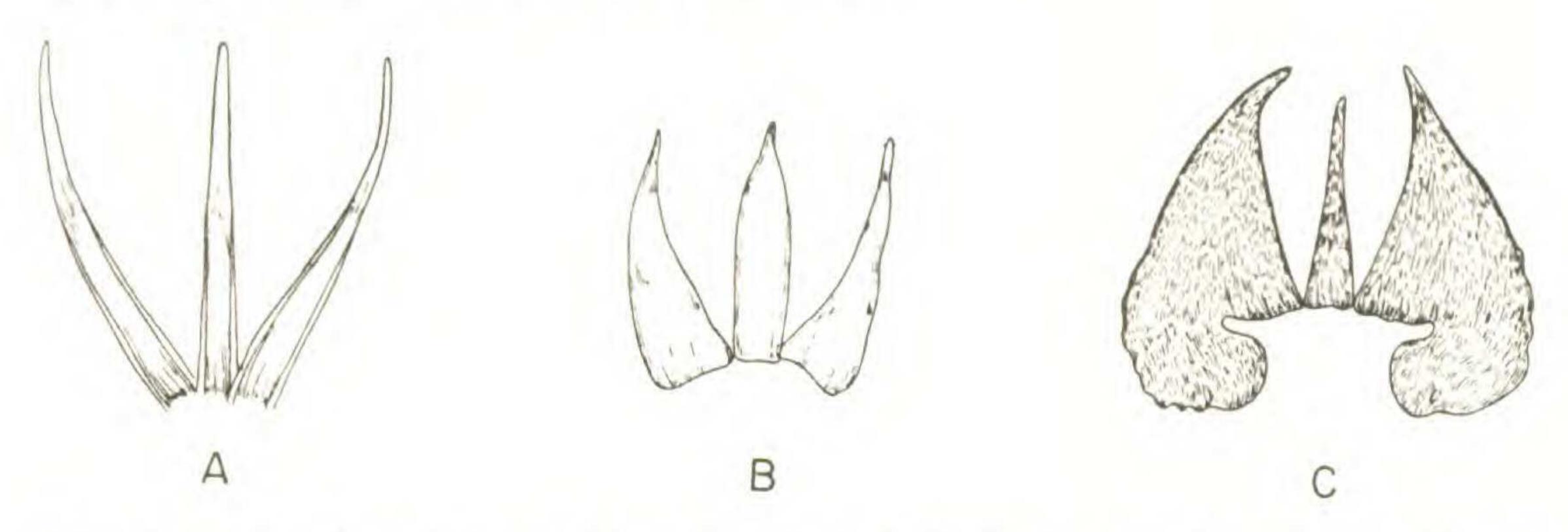
Type species: Phyllanthus niruri L.

In its present limited circumscription, sect. *Phyllanthus* comprises about 50 species, including most of the widespread weedy species in the genus. As pointed out previously (Contr. Gray Herb. 176: 51. 1955) the broad concept of the section held by Mueller and by Pax and Hoffmann (Naturl. Pflanzenf. 2 ed. 19c: 64. 1931) was unnatural, many unrelated plants being grouped together on the basis of the single criterion of three stamens with more or less horizontally dehiscing anthers. This artificial sect. *Euphyllanthus* in fact included representatives of six of the eight subgenera now recognized in the West Indies! As presently constituted, however, there

^{*} Continued from volume XXXVIII, p. 198.

can be little doubt that sect. *Phyllanthus* is a phylogenetically natural group, the members of which (with the exception of a few aberrant forms) appear to be the descendants of some common ancestor. It appears probable that this progenitor was an herbaceous species of subg. *Kirganelia* such as *P. tenellus*. This species resembles the West Indian species of sect. *Phyllanthus* in so many ways that it can be positively excluded only on the basis of its five stamens.

Within sect. Phyllanthus there are many species which appear extremely similar, at least on casual inspection, so that there has been much confusion in the application of names and circumscription of taxa. The resulting uncertainty has been compounded by the fact that due to the vagaries of human transport, exotic and native weedy species of Phyllanthus grow together in many tropical areas. A few of the particularly successful weeds have become so widely dispersed that it is now difficult or impossible to pinpoint their place of origin. However, the majority of species have more restricted ranges, and the three major species groups, or subsections, here recognized have characteristic geographical distributions. Only subsect. Swartziani, with representatives in America, Africa, and India, has a nearly cosmopolitan range; subsect. Niruri appears to be entirely American (though a few West African species may prove to belong here) and subsect. Pentaphylli is essentially restricted to the West Indies. It is striking that there are no indigeous members of sect. Phyllanthus in China, Australasia (except for the doubtful P. lacunarius), and the Pacific Islands; in these areas their place is occupied by habitally similar representatives of sects. Urinaria and Eriococcus.



Text-fig. 10. Diagrams of the cataphylls characteristic of the subsections of sect. *Phyllanthus*: A. Subsect. *Niruri* (*P. niruri*). B. Subsect. *Swartziani* (*P. amarus*). C. Subsect. *Pentaphylli* (*P. pentaphyllus*). The cataphylls are shown in dorsal view as they would appear if spread out, with the stipules brought into the plane of the blade.

As indicated in the synoptic key, the three subsections are easily separated by distinctive types of cataphyllary stipules (cf. Text-fig. 10). Although three distinctive types of pollen grains also occur, these are not entirely correlated with the subsectional divisions. Subsection *Niruri*, indeed, has distinctive elongated 4-colporate grains (PLATE VIII, fig. 34); but the grains in subsect. *Swartziana* are precisely like those of most

species of subsect. *Pentaphylli* (i.e., similar to PLATE VIII, fig. 37). However, two species of the latter subsection, *P. leptoneurus* and *P. dimorphus*, have coarsely reticulate pollen grains (PLATE VIII, fig. 35), although in other respects they are obviously closely related to adjacent species in subsect. *Pentaphylli*. The causes of these differences in pollen morphology do not appear at all clear.

SYNOPTIC KEY TO THE SUBSECTIONS AND SPECIES

- 1. Cataphyllary stipules thin and membranous or scarious (not indurate), not auriculate at the base or only very inconspicuously so.
 - Cataphyllary stipules linear-lanceolate; branchlet stipules more or less involute; leaves conspicuously oblique at the base; stamens 3, the filaments free or united below; pollen grains prolate, 4-colporate; seeds verruculose.
 - 3. Branchlets with c. 15-30 leaves, these 7-15 mm. long; male flowers 3-7 per cymule; calyx-lobes 1.2-1.5 mm. long; filaments 0.6-0.9 mm. long, connate below into a column; seeds 1.4-1.6 mm. long.

 16. P. niruri
 - 3. Branchlets with c. 35-45 leaves, these 4-6 mm. long; male flowers 1 per cymule (usually accompanied by a bud); calyx-lobes 0.6-0.8 mm. long; filaments 0.25-0.35 mm. long, free; seeds 0.95-1 mm. long.
 - 2. Cataphyllary stipules broader; branchlet stipules not involute; leaves scarcely if at all oblique at the base; stamens 2 or 3, the filaments free to wholly united; pollen grains ellipsoidal, 3-colporate; seeds striate or ribbed.

 Subsect. 11b. Swartziani.
 - 3. Seeds with 5-7 longitudinal ribs; weedy annual herbs.
 - 4. Cymules unisexual; calyx-lobes obtuse.
 - 5. Branchlets smooth; stem often angled; leaves usually narrowed to a point at the tip; female disk subentire; styles spreading and appressed.

 18. P. debilis
 - 3. Seeds with c. 9-12 very delicate scarcely raised longitudinal striae.
 - 4. Filaments partially united; pedicel of female flower 1.5-2.5 mm. long; herbs.
 - 5. Style-branches peculiarly thickened, similar to the arms of a unusually modified; branchlets mostly with 15-30 leaves; stamens usually 3; female calyx-lobes 1.2 mm. long or more in fruit.

 - 6. Filaments united only in the lower half; female disk divided

into 3 linear segments; leaves narrowed toward the tip; seeds just under 1 mm. long; Lesser Antilles.

22. P. caribaeus

- 5. Style-branches peculiarly thickened, similar to the arms of a Maltese cross; branchlets mostly with 30-60 leaves; stamens usually 2; female calyx-lobes 0.75-1 mm. long in fruit; Cuba.

 23. P. procerus
- 4. Filaments free; pedicel of female flower becoming 3-3.5 mm. long; stem woody; Jamaica. 24. P. fadyenii
- 1. Cataphyllary stipules becoming dark reddish or blackish, indurate, conspicuously auriculate at the base; mostly perennials.

subsect. 11c. Pentaphylli-

- 2. Midrib of male calyx-lobes not dorsally carinate.
 - 3. Plants with a single main stem or, if stems clustered at the base, these subsimple, not repeatedly branching (cf. Plate XXII, B); branchlets with mostly 20–50 leaves (or more); leaves linear to oblong or elliptic, never scabridulous beneath (hispidulous in *P. amnicola*); apical centimeter of stem with c. 3–7 evident branchlets [including any immature branchlets with evident leaf primordia]; stamens 2 or 3.
 - 4. Staminal column 0.2-0.5 mm. long; leaves various; pollen grains finely reticulate.
 - 5. Anthers extrorse, dehiscing horizontally or obliquely.
 - 6. Calyx-lobes 5; stamens 2; dioecious perennial with linear leaves; Cuba. 25. P. micranthus
 - 6. Calyx-lobes usually 6 (at least those of male flower); stamens always 3; monoecious or dioecious, leaves broader; Hispaniola.
 - 7. Branchlets and leaves smooth, never hispidulous; filaments usually united 2/3 their length or more.
 - 8. Branchlet stipules scarious, becoming reddish but not blackened and indurate; leaves membranous to chartaceous; disk-segments of male flower smooth or slightly glandular-crenulate.

 - 9. Anthers sessile, compressed together or connate by the connectives, dehiscing horizontally; branchlets mostly 1–5 cm. long; leaves mostly 2.5–4 mm. long; dioecious, with several erect stems from a caudex. 27. P. brachyphyllus
 - 8. Branchlet stipules becoming blackened and indurate; leaves coriaceous; disk-segments of male flower conspicuously rugose-papillate; dioecious perennial.

 28. P. buchii
 - 7. Branchlets and undersurfaces of leaves conspicuously white-hispidulous; filaments united in the lower half; dioecious herb rooting at the nodes. 29. P. amnicola

- 5. Anthers introrse, dehiscing more or less vertically; stamens 2; Cuba. 30. P. maestrensis
- 4. Staminal column (0.5-) 0.7-1.3 mm. long; leaves oblong to linear, with broadly rounded to truncate tips; pollen grains coarsely reticulate; dioecious or subdioecious perennials.
 - 5. Anthers sessile but not completely confluent; staminal column 0.5-0.9 mm. long; styles up to 0.5 mm. long; leaves membranous to chartaceous; Hispaniola. 31. P. leptoneurus
 - 5. Stamens completely fused, the anthers confluent in a circumscissile synandrium; staminal column 1.1–1.3 mm. high; styles 1.1–1.7 mm. long; leaves subcoriaceous; Cuba.

32. P. dimorphus

- 3. Plants without a single main stem, the branches clustered on a caudex, simple or repeatedly branching below (cf. Plate XXII, C); branchlets with mostly 5-25 leaves; leaves mostly elliptic to obovate or sub-orbicular; apical centimeter of stem usually with only 1-3 evident branchlets; stamens normally 2.
 - 4. Leaves areolate-foveolate above; capsule 3.5 mm. in diameter, the seeds c. 1.4–1.7 mm. long; dioecious; Cuba. 33. P. junceus
 - 4. Leaves not areolate above; capsule and seeds smaller; usually monoecious.
 - 5. Leaves not scabridulous above; seeds 0.8-1 mm. long, the epidermal cells slightly hygroscopic; widespread 34. P. pentaphyllus
 - 5. Leaves scabridulous on both sides.
 - 6. Suffruticose; female disk cupuliform; seeds 1.–1.1 mm. long, the epidermal cells not appreciably hygroscopic; eastern Cuba.

 35. P. pulverulentus
- 2. Midrib of calyx-lobes dorsally carinate; psammophilous microphyllous herbs, stamens 2; Isle of Pines.
 - 3. Erect, with the habit of a miniature tree; leaves elliptic to obovate, rounded at the base; male disk-segments subentire; female flower definitely pedicellate (pedicel 0.6-1.4 mm. long) 37. P. selbyi
 - 3. Prostrate herb with habit of *Euphorbia* (*Chamaesyce*) spp.; leaves ovate, subcordate or cordate at base; male disk-segments rugose-papillate; female flower subsessile (pedicel only 0.3 mm. long or less).

 38. P. imbricatus

Subsect. 11a. Niruri Webster, Contr. Gray Herb. 176: 52. 1955.

Annual herbs; cataphyllary stipules linear-lanceolate; branchlet stipules involute; leaves inequilateral at the base; monoecious, cymules unisexual; stamens 3, filaments free or united below, pollen grains 4-colporate, heteroreticulate; disk of female flower patelliform or cupuliform; styles free, the tips capitate; seeds verruculose.

Type species: Phyllanthus niruri L.

This entirely American group includes a small number of species, of which by far the most widespread is *P. niruri*. This species is so variable that it can scarcely be delimited from most of the related proposed species, such as *P. chlorophaeus* Baill. of Mexico; further study will be necessary to determine the status of these latter. However, there do appear to be at least two valid species in addition to *P. niruri*: *P. mimicus* of Tobago and *P. rosellus* (Muell. Arg.) Muell. Arg. of Brazil.

The very narrow stipules, oblique leaf base, and distinctive pollen grains clearly distinguish this subsection in the West Indies. However, there are some South American species such as *P. microphyllus* which have pollen grains somewhat transitional between those of the present group and subsect. *Swartziani*. Furthermore, there are a few West African species such as *P. benguelensis* which greatly resemble *P. niruri* and may prove to be related. A re-evaluation of the subsectional limits may thus be necessary when the species from these two areas are studied critically.

16. Phyllanthus niruri L. Sp. Pl. 981–982. 1753; ssp. niruri. (PLATE XIX, figs. A-B).

Niruri barbadense . . . petiolis florum brevissimis Rand, Trans. Roy. Soc. 35: 295. 1727; Martyn, Hist. Pl. Rar. pl. 8. 1728.

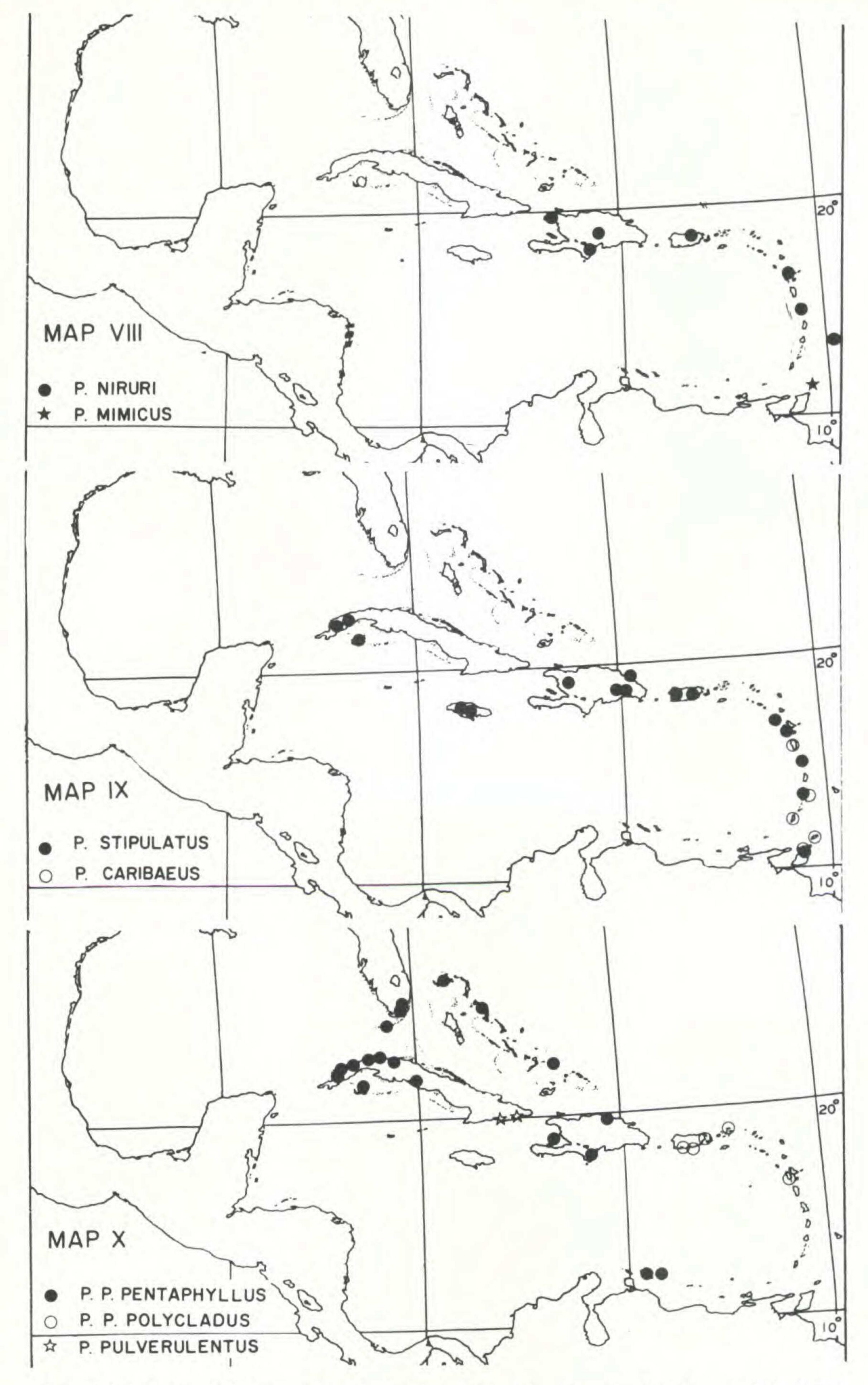
Phyllanthus foliis alternis alternatim pinnatis &c. L. Hort. Cliffort. 439. 1738 (excl. ref. Burm. & Rheede).

Urinaria erecta Medic. Monadelph. 81. 1787.

Phyllanthus lathyroides a commutatus Muell. Arg. Linnaea 32: 41. 1863; DC. Prodr. 15(2): 403. 1866 (ex p.).

Diasperus niruri (L. "em.") O. Ktze. Rev. Gen. 2: 600. 1891.

Annual herb; primary stem simple or considerably ramified, 1.5-5 dm. high, 1-2.5 mm. thick, olivaceous, smooth, terete; internodes mostly 1-4 cm. long. Cataphylls: stipules narrowly lanceolate, (1.5-) 1.8-2.5 (-3) mm. long, acuminate, truncate at the base, entire, scarious, olivaceous with reddish tips, turning brownish; blade often fused laterally with the stipules in the lower half. Deciduous branchlets mostly 5-10 cm. long, 0.3-0.5 mm. thick, olivaceous, smooth, more or less terete, with c. 15-30 leaves; first internode (3.5-) 5-10 (-13) mm. long, median internodes 2.5-5 mm. long. Leaves: stipules narrowly linear-lanceolate, unequal, the longer of each pair 2-2.7 mm. long, the shorter 1-1.7 mm. long; both narrow (0.15-0.25 mm. broad) and canaliculate at base due to the involute scarious entire margins; tip filiform-acuminate, often reddish-tinged. Petioles 0.4-0.7 mm. long. Leaf-blades thin, smooth on both sides, asymmetrically ovate or elliptic, mostly 7-15 (-17) mm. long, (3-) 4-8 (-9) mm. broad, acute or subacute at the tip, conspicuously oblique at the base (i.e., acute on one side and rounded on the other); above dark green, the midrib and laterals apparent but not raised; beneath conspicuously pallid, the midrib prominently raised, the laterals (4-7 on a side) fairly



MAPS VIII-X. Distribution of some species of sect. Phyllanthus in the West Indies (mainland stations of P. niruri and P. stipulatus not shown).

conspicuous, connecting intramarginally, the tertiary veinlets forming an obscure reticulum; margins smooth or obscurely roughened, sometimes slightly thickened.

Monoecious; branchlets with the (0-) 1-2 (-4) proximal nodes barren, the succeeding (2-) 3-6 (-8) nodes with racemiform cymules of 3-7 successively maturing male flowers, the remaining distal nodes with soli-

tary female flowers.

Male flower: pedicel 1.2–1.8 mm. long. Calyx-lobes 5 (rarely 6), obovate or obcuneate, 1.2–1.5 mm. long, (0.8-) 1–1.5 mm. broad, obtuse or rounded to nearly truncate at the tip, entire, membranous, yellowishwhite or sometimes slightly reddish-tinged at the base, dorsally carinate along the midrib; midrib with a few steeply ascending often obscure lateral veinlets. Disk-segments 5, broadly cuneate, 0.25–0.4 mm. across, obscurely to conspicuously glandular-papillate. Stamens 3; filaments c. 0.6–0.9 mm. long, united 2/3 to 3/4 their length into a slender column, the free portions of the filaments very slender; anthers 0.25–0.4 mm. long, 0.3–0.45 mm. broad, anther-sacs nearly parallel, the slits apically convergent, dehiscing obliquely; pollen grains prolate, 4-colporate, 38–48 μ long, 25–34 μ broad.

Female flower: pedicel (2–) 2.5–4 (–4.5) mm. long, olivaceous or stramineous, smooth, below terete, above thicker and angled due to the decurrent midribs of the calyx-lobes. Calyx-lobes 5, broadly elliptic or obovate (1.5–) 1.7–2.3 (–2.7) mm. long, (1.2–) 1.3–1.8 mm. broad, obtuse or rounded at the tip, entire, olivaceous with rather broad whitish scarious margins (sometimes inconspicuously reddish at the base), the dorsally carinate midrib with 4–5 steeply ascending lateral veins on each side. Disk patelliform, obscurely 5-angled, rather massive, the angles slightly upturned. Styles free, more or less ascending and arching, c. 0.5–0.6 mm. long, bifid, the branches spreading and recurved, stigmas capitate.

Capsules oblate, c. 3 mm. in diameter, stramineous, reticulate-veiny. Seeds 1.4–1.5 (–1.6) mm. long, 1.15–1.3 mm. radially and tangentially, fuscous when mature, densely covered with dark raised points; hilum triangular, c. 0.25–0.3 mm. across.

Flowering and fruiting throughout the year.

Type: Herb. Hort. Cliffort. (BM, Holotype). The typification of *P. niruri* and other details of its nomenclatural history have been discussed elsewhere (Jour. Arnold Arb. 37: 4–6, 13. 1956) and need not be repeated here.

DISTRIBUTION: ssp. *niruri* appears to be endemic to the West Indies (MAP VIII); the very similar ssp. *lathyroides* is widespread from Texas south through mainland tropical America into Argentina.

HAITI. Nord-ouest: coffee plantation, Jean Rabel, E. C. & G. M. Leonard 13746 (NY, US).

DOMINICAN REPUBLIC. Santiago: Valle del Cibao, Santiago, Hato del

Yaque, irrigation ditches, Ekman H16022 (A, S, US), H16515 (S). La Vega: Constanza, El Salto de Constanza, Jiménez 2971 (US). Barahona: near Barahona, Fuertes 89 ex p. (F, GH; mixed with P. amarus).

PUERTO RICO. San Juan: Bayamon, Millspaugh 320 (F, NY); cultivated ground, Catano, Britton, Britton, & M. S. Brown 6995 (NY); Rio Piedras, Johnston 215 (NY); clearing, limestone hillside, Pueblo Viejo, Britton & Boynton 8201 (NY); Santurce, in sand, Heller & Heller 4 (NY, US).

LESSER ANTILLES. GUADELOUPE: dans les champ de manioc, &c., Camp Jacob, Tombe-Novie, Duss 2921 (F, GH, NY, US); 1839, Beaupertuis (P). Martinique: dans les champs de cannes, Vaillant, Carbet, Fort de France, Duss 47 ex p. (F [mixed with P. amarus], GH, NY [mixed with P. tenellus]); Herb. L. C. Richard (P). Barbados: 1918, Freeman 5015 (F); among grass along roads, Forster Hall, Eggers 7185 (P).

The West Indian population of *P. niruri* is of historical interest, since it (as ssp. *niruri*) represents at once the type of the species and of the genus. The type locality is the island of Barbados, from whence the plant was brought to England and subsequently given to Linnaeus probably

by Philip Miller.

Subspecies *niruri* differs from the mainland populations of the species — which for the present may all be grouped under ssp. *lathyroides* — in the characteristically ovate or broadly elliptic leaves and especially in the pinnately veined calyx-lobes of the male flower. However, it must be admitted that these distinctions are very weak. The leaf-shape of the Antillean plants can be matched by various mainland plants, and it is possible that pinnate male calyx-lobes may be observed in specimens from Central or South America, although examination of about thirty mainland specimens has shown only unbranched midribs in the calyx-lobes.

The distribution of ssp. *niruri* in the West Indies is spotty, and it has usually been collected in cultivated fields, clearings, or along ditches. It is very difficult to determine what part of the present range should be considered indigenous, although it may be reasonably presumed that the plant was native at least to the Lesser Antilles before the first colonists

arrived.

Although *P. niruri* has been confused in the literature with *P. amarus*, the plant with which it is most easily confounded is probably *P. stipulatus*. Some forms of the latter species are similar in aspect, but it has usually smaller leaves not oblique at the base, different stipules, stamens with the filaments completely united, fruiting pedicels not over 2.5 mm. long, and striate rather than verruculose seeds.

17. Phyllanthus mimicus Webster, Contr. Gray Herb. 176: 52. 1955. (PLATE XIX, figs. C-D).

Slender erect annual herb; primary stem simple, 0.7–3.5 dm. high, 0.5–2 mm. thick, stramineous, smooth, terete; internodes mostly 1–2.5 cm. long. Cataphylls: stipules narrowly lanceolate, 1–1.5 mm. long, c. 0.25 mm. broad, attenuate-acuminate, thin and scarious, brownish; blade

narrower, c. 1–1.5 mm. long. Deciduous branchlets 3–6 cm. long, 0.15–0.2 mm. thick, olivaceous, minutely scabridulous, obscurely or acutely angled, with c. 35–45 leaves; first internode 3–5 mm. long, median internodes c. 1 mm. long. Leaves: stipules narrowly lanceolate, scarious, more or less involute (as in *P. niruri*), unequal, the longer of each pair c. 1.3–1.8 mm. long, the shorter 0.7–0.8 mm. long, the tip attenuate. Petioles 0.2–0.25 mm. long. Leaf-blades membranous, minutely scabridulous on both sides, mostly oblong, 4–6 mm. long, 1.5–2.5 mm. broad, obtuse-apiculate at the tip, conspicuously oblique at the base; above olivaceous, the midrib raised and minutely roughened; beneath very pale, the midrib raised, the laterals (4 or 5 on a side) ascending, connecting intramarginally, tertiary reticulum obscure; margins thin, plane, smooth or nearly so.

Monoecious, not all branchlets floriferous; proximal 8–15 nodes barren, succeeding 11–14 nodes with male flowers, the distal nodes bearing female flowers; flowers solitary, but the male often accompanied by an abortive bud.

Male flower: pedicel 1.7–2.3 mm. long. Calyx-lobes 5, obovate, 0.6–0.8 mm. long, 0.5–0.65 mm. broad, obtuse, yellowish and scarious, the unbranched midrib slightly dorsally carinate. Disk-segments 5, cuneate, c. 0.2–0.25 mm. across, obscurely glandular-crenulate. Stamens 3; filaments free, slender, c. 0.25–0.35 mm. long; anthers c. 0.2–0.25 mm. broad, anther-sacs divaricate, the slits apically contiguous but not confluent, dehiscing horizontally; pollen grains prolate, 4-colporate, 27–32 μ long, 17–19 μ broad.

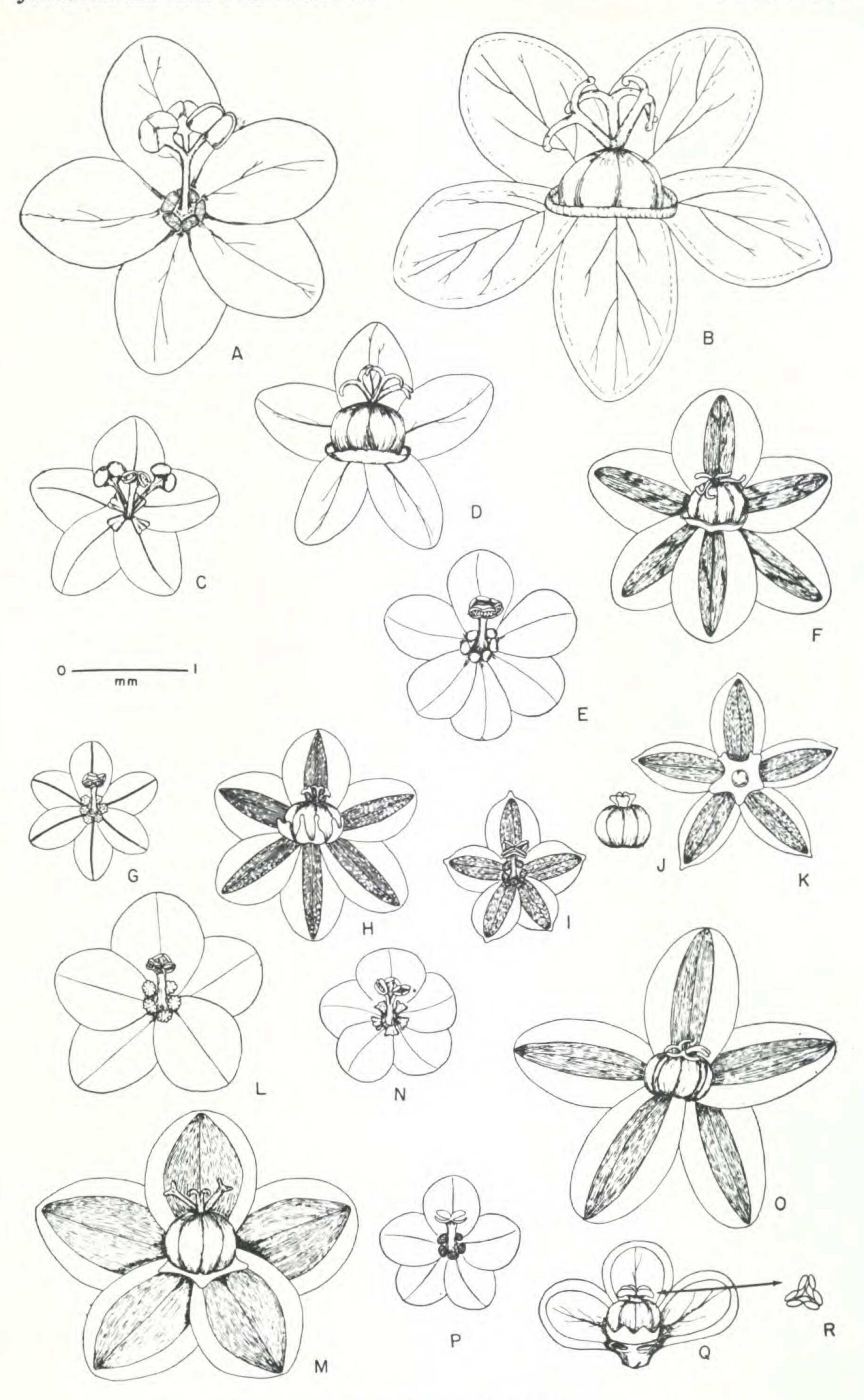
Female flower: pedicel 1.7–2 mm. long, stramineous, minutely scabridulous, terete below, obscurely angled above. Calyx-lobes 5, obovate, (1.3–) 1.5–1.7 mm. long, 0.6–0.9 mm. broad, obtuse, herbaceous with narrow scarious margins, the dorsally carinate midrib sparingly branched. Disk patelliform, roundly 5-angled, not thickened. Styles free, ascending, c. 0.25 mm. long, bifid, the branches recurving, the tips capitate.

Capsule oblate, c. 1.9–2 mm. in diameter, stramineous, obscurely reticulate-veiny. Seeds [all observed immature] c. 0.95–1 mm. long, 0.7 mm. radially and tangentially, with evenly spaced reddish-brown points.

Type: Tobago, Big River Bridge, Mason Hall, on a shaded bank, 13 Sept. 1909, Broadway 3038 (G, HOLOTYPE; F, MO, NY, S, ISOTYPES).

DISTRIBUTION: known only from the type locality (MAP VIII).

PLATE XIX. Flowers of Sect. Phyllanthus, Subsects. Nituri and Swartziani. Figs. A-B. Phyllanthus nituri L. ssp. nituri (Duss 47 [GH]). Figs. C-D. Phyllanthus mimicus Webster (Broadway 3038 [G]). Figs. E-F. Phyllanthus debilis Klein ex Willd. (Boeea 8313 [A]). Figs. G-H. Phyllanthus fraternus Webster (Collins 225 [GH]). Figs. I-K. Phyllanthus amarus Schum. & Thonn. (Wilson 7802) [GH]); female flower with ovary removed to one side. Figs. L-M. Phyllanthus stipulatus (Raf.) Webster (Howard & Howard 9895 [GH]). Figs. N-O. Phyllanthus caribaeus Urb. (Hodge 2425 [GH]). Figs. P-Q. Phyllanthus procerus Wright (Killip 42789 [US]).



Webster, West Indian Phyllanthus

This diminutive plant has received the epithet mimicus because of its extraordinary vegetative resemblance to P. caribaeus, which also occurs in Tobago. However, in all important respects (viz., narrow stipules, oblique leaf-bases, 4-colporate pollen grains, and verruculose seeds) it certainly agrees with subsect. Niruri rather than with the subsection (Swartziani) to which P. caribaeus belongs. In fact, P. mimicus resembles P. niruri in so many ways that some observers might prefer to regard it as a subspecies of P. niruri. The problem of specific distinctions in subsect. Niruri is especially acute because of the great variability of P. niruri. The mainland populations of that species have received several specific names (listed in Jour. Arnold Arb. 37: 13. 1956), but most of these certainly cannot be maintained. However, P. mimicus differs from all other variants of P. niruri heretofore observed in its very small flowers, reduced male inflorescence, and branchlets with 35-45 leaves. Therefore, at least until a thorough survey of variation within P. niruri has been made, it appears proper to maintain P. mimicus as a distinct species, even though its phylogenetic derivation as a reduced insular counterpart of the wide-ranging P. niruri is obvious.

Subsect. 11b. Swartziani Webster, Contr. Gray Herb. 176: 53. 1955.

Annual or perennial herbs; cataphyllary stipules triangular to lanceolate, scarious, not indurate nor auriculate at base; leaves equilateral at base or very nearly so; branchlet stipules not involute; monoecious, cymules unisexual or bisexual; stamens 2 or 3, filaments partially or wholly united; pollen grains ellipsoidal, 3-colporate, finely reticulate; disk of female flower patelliform and angled, or variously lobed or dissected; styles free, the tips slender or somewhat thickened (but not capitate); seeds longitudinally ribbed or striate, or transversely barred.

Type species: *Phyllanthus swartzii* Kostel. [=P. amarus Schum. & Thon.]. The choice of subsectional name now appears to have been unfortunate; but at the time it was not realized that P. swartzii was a later synonym of P. amarus.

This subsection comprises about 20 closely related species which are distributed in America, Africa, and India. There has been much confusion in the interpretation of these plants, many of which are widespread weeds. However, at least in tropical America the species can be easily distinguished by attentive inspection; they are all clear-cut entities, and there is no evidence of hybridization in the West Indies. In Africa and India, where the majority of the species occur, identifications are apt to be much more difficult, and intergradation between different species may occur.

The West Indian representatives of subsect. Swartziani fall into three different categories: (1) exotic weeds—P. fraternus and P. debilis; (2) indigenous weeds—P. amarus and P. stipulatus; and (3) West Indian endemics—P. caribaeus, P. fadyenii, and P. procerus. The last species

is a particularly interesting one, since it forms a connecting link with subsect. *Pentaphylli*; but the phylogeny of subsect. *Swartziani* as a whole cannot be considered here on the basis of the fragmentary representation in the West Indies.

18. Phyllanthus debilis Klein ex Willd. Sp. Pl. 4: 582-583. 1804. (PLATE XIX, figs. E-F).

Phyllanthus niruri γ javanicus Muell. Arg. Linnaea 32: 43. 1863; DC. Prodr. 15(2): 407. 1866.

Phyllanthus niruri & debilis ("Willd.") Muell. Arg. ibid.

Phyllanthus debilis "Herb. Ham." ex Hook. f. Fl. Br. Ind. 5: 299. 1887.

Erect annual herb (sometimes becoming woody at the base) c. 1-7.5 dm. high, the main stem often branching in age, mostly 1-2.5 mm. thick, above usually sharply angled and compressed, becoming subterete below, smooth, olivaceous, with internodes 0.5-5 cm. long. Cataphylls: stipules triangularlanceolate, (1.2-) 1.4-1.8 (-2) mm. long, 0.6-1 mm. broad, acuminate, entire, truncate or with one side somewhat dilated at the base, olivaceous with an ill-defined scarious margin; blade narrowly lanceolate, acuminate, (1-) 1.4-1.8 mm. long. Deciduous branchlets mostly 4-10 (-12) cm. long, 0.3-0.5 mm. thick, sharply angled and sometimes compressed, quite smooth, olivaceous, with mostly 15-35 leaves; first internode 5-15 mm. long, median internodes 2.5-4.5 mm. long. Leaves: stipules lanceolate, mostly 0.9-1.2 mm. long (proximal ones sometimes longer) and 0.2-0.3 mm. broad, acuminate, entire, olivaceous with yellowish-white scarious margins, carinate along the midrib. Petioles 0.3-0.7 (-1) mm. long. Leaf-blades membranous to chartaceous, smooth on both sides, narrowly elliptic (in West Indian specimens), (6-) 8-20 mm. long, 2.5-5 mm. broad, acute or subacute at the tip, acute at the base; above dark green, all nerves except the midrib obscure; beneath greyish or brownish, the midrib prominent, the chief laterals (c. 4 or 5 on a side) somewhat raised, connecting intramarginally, the tertiary veinlets completely obscure; margins plane, unthickened, smooth.

Monoecious; cymules unisexual. Proximal 2-4 nodes of branchlet with racemiform cymules of c. 3 or 4 male flowers, distal nodes with solitary female flowers; bracteoles yellowish-white, scarious, persistent.

Male flower: pedicel less than 0.5 mm. long. Calyx-lobes 6, biseriate, subequal, obovate to obcuneate, 0.5–0.6 mm. long, 0.45–0.6 mm. broad, broadly rounded to subtruncate or retuse at the tip, entire, membranous, the midrib unbranched. Disk-segments 6, roundish to obcuneate, entire, thin, not glandular, c. 0.15–0.2 mm. across. Stamens 3, the filaments completely connate into a rather slender column 0.25–0.3 mm. high; anthers sessile atop the column, discrete or partially connate by the connectives, deltoid, blunt, c. 0.1–0.15 mm. long, 0.2–0.25 mm. broad; anther-sacs divergent, the slits confluent, dehiscing horizontally; pollen grains finely reticulate, 21– $23~\mu$ long, 17– $20~\mu$ broad.

Female flower: pedicel becoming 1.1-1.6 mm. long, usually conspicu-

ously angled, dilated above, smooth, olivaceous. Calyx-lobes 6, obovate, (1–) 1.2–1.5 mm. long, (0.5–)0.75–1 mm. broad, rounded at the tip, with very broad whitish scarious margins (the green midstrip less than a third the breadth of the lobe), the midrib unbranched. Disk patelliform, entire or obtusely and shallowly 6-lobed, sometimes crenulate between the lobes. Styles free, spreading, appressed to the ovary (at least at the tips), c. 0.2–0.3 mm. long, bifid about to the middle, the arms divergent, the slender unthickened tips recurved.

Capsule oblate, very rounded in outline, c. 2–2.2 mm. in diameter, reddish-brown, smooth, veins completely obscure. Seeds trigonous, light yellowish-brown, c. 1–1.1 mm. long, 0.75–0.85 mm. radially and tangentially, with c. 6 or 7 straight longitudinal ribs and many fine transverse striae on the back.

Type: India, Madras, Tranquebar, in rice-fields, February 1799, *Klein* (B, Syntypes; photographs examined). Through the courtesy of the director of the Botanical Institute, Berlin-Dahlem, photographs of three sheets of Klein's original collection (in the Willdenow Herbarium) have been given to the Arnold Arboretum. Although there is considerable variation in leaf size and shape among the type sheets, there is no doubt that a single species is represented and that it is indeed the plant that has been passing as *P. debilis* or *P. niruri* var. *debilis*.

DISTRIBUTION: native probably to southern India and Ceylon; introduced into Indonesia, the Pacific islands, and the West Indies.

LESSER ANTILLES. GUADELOUPE: Ste. Marie, Sous-le-Vent, Goyave, bananeraies recentes, alt. 60 m., 28 July 1936, Stehlé 1132 (NY); Petit Bourg, 12 Mar. 1936, Rodriguez 4901 (P).

The description is based on examination of the West Indian and the following additional collections:

INDIA: without locality, Herb. Wight, Wallich 7895D (K). Bombay: Concan, Stocks (GH, mixed with P. amarus). CEYLON: Peradeniya, de Silva 17 (A). INDONESIA. Java: Herb. Hasskarl (L); Buitenzorg, Hallier (L). Sumatra: Aer Djoman, Boeea 8313 (A). MICRONESIA. Bonins: Chichi Jima, Fosberg 31550 (US). Marianas: Saipan, Fosberg 25228 (US). Palau: Hosokawa 7494 (US); Koror, Fosberg 32066B (US). Ponape: Glassman 2556B (US). HAWAIIAN ISLANDS. Oahu: Honolulu, Degener 9118, 19286 (GH), Fosberg 10755 (A).

This species, a newcomer to the Caribbean, cannot be said to have established itself as part of the weedy flora; however, it seems proper to include it in the expectation that it may be introduced into additional islands in the future.

The circumscription of *P. debilis*, which is a rather widely dispersed weed, is attended by difficulties that unfortunately have not been entirely resolved in the present study. Together with *P. fraternus*, *P. rotundifolius*, and a few other related Old World plants, *P. debilis* belongs to a difficult

species complex which has still to be critically analyzed. Mueller had such a confused concept of several of these species that it has been most difficult to untangle his synonymy and the work of those who have followed his treatment. He considered the species *P. niruri* to be typified by the plant now known as *P. amarus* (his var. *genuinus*), while *P. debilis* and *P. fraternus* (plus the distantly related *P. pentaphyllus*!) were appended as varieties. Hooker, who had a clearer understanding of these plants, recognized *P. debilis* as distinct; but his description is inaccurate in some details.

The closest relative of P. debilis is undoubtedly P. fraternus, although the latter usually differs so much in aspect that it has more often been confused with P. amarus than with P. debilis. The nature of the relationship between P. debilis and P. fraternus will be discussed below under the latter species.

It seems probable that the *Kirganeli* of Rheede (Hort. Malabar. 10: 29, pl. 15. 1682) and the *Jatha-Aembula* of Hermann (ex Burman, Thes. Zeyl. 230. 1737), which have graced the synonymies of various species, actually represent *P. debilis*. Rheede's figure is characteristic, and when the known distribution of the various Indian species of sect. *Phyllanthus* are taken into account, it appears that he and Hermann are more likely to have had *P. debilis* than any other species.

19. Phyllanthus fraternus Webster, Contr. Gray Herb. 176: 53. 1955. (PLATE XIX, figs. G-H).

Phyllanthus scabrellus Webb in Hook. Niger Fl. 175-176. 1849; ex p. (excl. typ.).

Phyllanthus niruri β scabrellus Muell. Arg. Linnaea 32: 43. 1863; DC. Prodr. 15(2): 406. 1866, as γ scabrellus.

Phyllanthus niruri sensu Hook. f. Fl. Br. Ind. 5: 298. 1887 (ex p.); sensu Hutch. in Fl. Trop. Afr. 6(1): 731. 1912 (as to description).

Erect annual herb c. 1.5–4 dm. high, the main stem mostly 1–2 mm. thick, subterete, above with narrow sharp angles running longitudinally between the nodes, smooth, stramineous, the internodes c. 1–3 (–4) cm. long. Cataphylls: stipules lanceolate, 0.8–1.3 mm. long, 0.25–0.4 mm. broad, entire, truncate at the base (definitely not auriculate) pale and scarious; blade narrower. Deciduous branchlets (2–) 4–8 (–10) cm. long (0.3–) 0.4–0.5 mm. thick, subterete with a narrow sharp wing on either side, obscurely to densely scabridulous along the wing-edge and sometimes scabridulous between the wings as well, with mostly 10–30 leaves; first internode (8–) 10–18 (–23) mm. long, median internodes (1.5–) 2–3.5 mm. long. Leaves: stipules narrowly lanceolate, 0.7–1.2 mm. long, 0.15–0.3 mm. broad, acuminate, entire, whitish and scarious except for the narrow olivaceous midstrip. Petioles 0.3–0.6 mm. long. Leaf-blades membranous, smooth and glabrous, elliptic-oblong, 6–11 mm. long, 3–5 mm. broad, rounded at the tip, cuneate to obtuse at the base; above dark green, only

the plane midrib visible; beneath paler, greyish, the midrib somewhat raised, the laterals (4–7 on a side) conspicuous, ascending, connecting near the margin, the anastomosing tertiary veinlets forming a delicate (sometimes quite obscure) reticulum; margins unthickened, plane, smooth or minutely roughened.

Monoecious; cymules unisexual. Proximal (2-) 3-5 nodes of branchlet with male cymules of 2 or 3 flowers; succeeding nodes with solitary female

flowers; transitional node occasionally with a bisexual cymule.

Male flower: pedicel 0.25–0.5 mm. long. Calyx-lobes 6, subequal, elliptic to obovate, c. 0.4–0.6 (–0.7) mm. long, 0.3–0.5 (–0.6) mm. broad, obtuse or rounded at the tip, yellowish and scarious, the midrib unbranched. Disk-segments 6, more or less angled or lobed, obscurely glandular, c. 0.1 mm. broad. Stamens 3, filaments united into a column 0.1–0.25 mm. high; anthers sessile or subsessile atop the column, deltoid, obtuse, c. 0.1 mm. long, 0.15–0.2 mm. broad; anther-sacs divaricate, the slits apically confluent, dehiscing horizontally or nearly so; pollen grains finely reticulate, 19.5–25 μ long, 18–21.5 μ broad.

Female flower: pedicel becoming (1.3–) 1.5–2 mm. long, olivaceous, smooth, angled or subterete. Calyx-lobes 6, often unequal (one or two distinctly smaller than the others), narrowly obovate to linear-spathulate in fruit, (1–) 1.2–1.5 mm. long, 0.35–0.8 mm. broad, rounded to subacute at the tip, with broad scarious margins (the narrow herbaceous midstrip 1/3 the breadth of each calyx-lobe or less), the midrib unbranched. Disk an irregular cup deeply lobed or parted into 6–9 crenulate-lacerate segments. Styles only 0.1–0.15 (–0.2) mm. long, free, erect or ascending, very briefly bifid at the tip, the style-branches blunt, about as thick as long, recurving.

Capsule oblate, c. 2.1 mm. in diameter, stramineous or reddish-brown, smooth, the veins completely obscure. Seeds c. 0.95–1.1 mm. long, 0.7–0.8 mm. radially and tangentially, light yellowish-brown, with c. 6 or 7 straight (only rarely anastomosing) slightly elevated longitudinal ribs and many fine transverse striae on the back.

Type: India, Punjab, Tummooghat, Ravee-Chenab Doeb, Oct. 1846, Thomas Thomson (K, Holotype; GH, Isotype). A word of clarification is necessary regarding the typification of this species. Mueller (Linnaea 32: 43. 1863; DC. Prodr. 15[2]: 405–406. 1866) referred P. scabrellus Webb partly to P. rotundifolius Klein ex Willd. and partly to P. amarus ("P. niruri") as var. scabrellus. It might be concluded that in the latter case he was transferring Webb's name and that the type of Webb's species would belong with the present plant; if such were the case, then the species described above would have to be called P. scabrellus. However, it is quite clear from Webb's description and citation of specimens that his proposed species was based mainly on specimens of P. rotundifolius (e.g., St. Jago, Cape Verde Islands, Hooker [GH, Syntype]) and that he merely cited incidentally the Perrottet specimen which represents P. fraternus. Mueller

thus in publishing Perrottet's plant as a variety of *P. niruri* adopted Webb's epithet but in such a manner that it evidently must be treated as a new name.

DISTRIBUTION: native probably to West Pakistan and western India; introduced into Africa and the West Indies.

BERMUDA: weed in field, Collins 225 (GH, NY); Smith's Parish, roadside at church, Degener 995 (A); Hotel Frascati, Moore 2973 (GH). CUBA: low pine woods, El Salado [prov. Pinar del Río?], Wright 1675 ex p. (NY, mixed with P. procerus). BARBADOS: Freeman 215 (NY); W. Wright (BR, annotated by Mueller as P. niruri var. genuinus). TRINIDAD: Finlay (TRIN 2461); in Dr. Finlay's garden, Kuntze 989 (NY).

The description is based on examination of the type collection, the West Indian specimens cited above, and the following:

INDIA: "East India", Roxburgh [Hb. Forsyth] (K). Bengal: Griffith (GH). Kumaon: Bagesar, Strachey & Winterbottom 2 (GH).

A prolonged study of the available specimens of the complex which Mueller included in his "P. niruri" has made it clear that I acted too hastily in reducing P. fraternus to the status of a synonym of P. as perulatus Hutch. This disposition (Jour. Arnold Arb. 37: 8. 1956) was made after comparison with the type (Schlechter 11866, Komati Poort, Transvaal [K]); but later more detailed study of a duplicate sheet in the Gray Herbarium indicates that P. fraternus and P. asperulatus are by no means identical and had best be kept separate for the time being. The plant collected by Schlechter differs from P. fraternus in its slightly longer fruiting pedicels and especially in its entire female disk and spreading styles. In the latter two characters, indeed, P. asperulatus agrees much better with P. debilis, although its leaf shape and scabridulous branchlets suggest P. fraternus. From both P. debilis and P. fraternus, P. asperulatus differs in the broader green midstrip of its calyx-lobes; but this is admittedly not a very convincing distinction. Unfortunately, no seeds of P. asperulatus have been seen; these might possibly furnish additional distinguishing characters. For the present, one can only conclude that P. asperulatus represents an entity closely related to both P. debilis and P. fraternus, but that its exact affinity cannot be determined at this time.

In the original publication of *P. fraternus* it was remarked that the species was rather closely related to *P. amarus*. Although that statement is correct as far as it goes, it should be made clear that the closest relative of *P. fraternus* is *P. debilis*. Typical specimens of the two differ so strongly in aspect (due to the more angled stems and narrower leaves of *P. debilis*) that on casual inspection the two species may appear to be very distinct. However, *P. debilis* proves to be so variable with respect to both angularity of stem and leaf shape that vegetative distinctions alone are insufficient to distinguish the two species. The very similar male flowers are so small that it is impossible to tell if any significant size differences exist; and the seeds appear almost identical. The only sure mark of distinction, there-

fore, lies in the female flowers; and here, too, the size of the floral parts is so small that measurement with a conventional binocular microscope is too inexact to reveal significant differences. Fortunately, certain qualitative characters are readily visible under low magnification: the disk of the female flower of P. fraternus is always deeply dissected into irregular segments, and the short styles are erect or at least ascending at a 45° angle, while the style-branches are very short and blunt. In contrast, the disk of the female flower of P. debilis is a shallow cup with a continuous rim which is merely angled or at most shallowly lobed; and the styles are appressed to the ovary (at least at the tips) and much more deeply parted. The erect vs. appressed character of the styles of the two species may be observed even in young buds, so that here it is not a feature which becomes highly modified during ontogeny (as is the case in some other species).

Although these characters of the female flower appear to be constant, so that they will serve dependably to separate the two species, it must be confessed that in the majority of features the two are extremely similar. It is possible that a future study, based on the examination of many more specimens from India than have been available here, may demonstrate that the two taxa should be considered subspecies of a single variable species (which might also include such forms as P. asperulatus). Supporting this possibility is the fact that specimens more or less intermediate between P. fraternus and P. debilis have been observed. One of these is the Griffith collection from "Bengal Presidency" cited above, which has vegetative features much as in P. debilis but which in floral characters agrees with P. fraternus. On the basis of the specimens cited and others examined at Kew (not referred to in the writing of the description), it appears that P. fraternus occupies a range chiefly in West Pakistan (Indus River valley) and northwestern India (Punjab and United Provinces), while P. debilis is mainly distributed from Bombay and Madras south to Ceylon, and also in Sikkim and Bhutan. Only in Bengal is it clear that the two come together, and it is here that the intermediate specimen occurs. This gives the impression of two allopatric subspecies of a single species which interbreed where brought together; but at present the documentation for this possibility is so slight that it appears most practical to retain P. debilis and P. fraternus, at least provisionally, as distinct species.

Phyllanthus fraternus has also been introduced into Africa, on the basis of at least one specimen examined (Senegal, Perrottet 755 [G]); and Hutchinson's description of "P. niruri" appears to be based mainly on the present species, although it has not been possible to check any of the other specimens cited. In the later treatment by Hutchinson & Dalziel (Fl. W. Trop. Afr. 1: 290–291. 1928) P. fraternus still appears as "P. niruri." In most of the tropics, however, P. fraternus is very much less common than P. amarus and so far has not been reported from South America, eastern Asia, or the Pacific Islands.

20. Phyllanthus amarus Schum. & Thonn. Kongl. Danske Vidensk. Selsk. Skr. 4: 195–196. 1829. (PLATE XIX, figs. I-K).

Fruticulus capsularis, hexapetalis &c. Pluk. Phytogr. 3: pl. 183, fig. 5. 1692. Phyllanthus urinaria sensu L. Sp. Pl. 982. 1753; ex p. (excl. typ.). Phyllanthus niruri sensu Sw. Obs. Bot. 354–355. 1791 (ex p.). Phyllanthus swarzii Kostel. Allgem. Med. Pharm. Fl. 1771. 1836. Phyllanthus niruri β genuinus Muell. Arg. in DC. Prodr. 15(2): 406. 1866. Non P. niruri L.

Phyllanthus nanus Hook. f. Fl. Br. Ind. 5: 298. 1887.

Erect annual herb (sometimes slightly woody at the base) 1-5 dm. high, the main stem simple or branched, smooth, terete, stramineous or brownish, c. 1.5-2 mm. thick; internodes mostly 1-3 cm. long. Cataphylls: stipules broadly deltoid, 1.3-2.1 mm. long, 0.6-1 mm. broad, acuminate, entire, scarious, brownish; blade subulate, acuminate, c. 1-1.5 mm. long. Deciduous branchlets 4-12 cm. long, c. 0.4-0.5 mm. thick, subterete (never winged or sharply angled), smooth or sometimes slightly scabridulous in the first internode, with c. 15-30 leaves; first internode 5-14 mm. long, median internodes c. 2-3 mm. long. Leaves: stipules ovatelanceolate or lanceolate, 0.8-1.3 mm. long, 0.2-0.4 mm. broad, acuminate (often attenuately so), scarious except for the narrow yellowish-green midstrip, entire. Petioles 0.3-0.5 mm. long. Leaf-blades membranous or somewhat thickened, usually elliptic-oblong (sometimes somewhat obovate), mostly 5-11 mm. long and 3-6 mm. broad, obtuse or rounded and often apiculate at the tip, obtuse or rounded and sometimes slightly inequilateral at the base; above bright green, the midrib raised, the laterals invisible; beneath greyish or glaucous, the midrib and laterals (c. 4 or 5 on a side) raised and conspicuous, the tertiary veinlets forming a delicate reticulum or sometimes obscure; margins plane, not especially thickened, smooth or obscurely and minutely roughened.

Monoecious; proximal (1-) 2 axils with unisexual cymules of (1-) 2 male flowers, all succeeding axils with bisexual cymules, each consisting of one male and one female flower.

Male flower: pedicel 0.6–1.3 mm. long. Calyx-lobes 5 (very rarely 6), subequal, ovate or elliptic, 0.3–0.6 mm. long, 0.2–0.55 mm. broad, abruptly acute, herbaceous with broad scarious margins, the midrib unbranched. Disk-segments 5, orbicular, c. 0.1 mm. in diameter, entire, not glandular. Stamens 3 (rarely 2); filaments completely connate into a column 0.2–0.3 mm. high; anthers sessile atop the column, one often reduced to a single anther-sac (or sometimes only 2 functional anthers present), 0.2–0.3 mm. broad; anther-sacs divergent, the silts completely confluent, dehiscing obliquely to less commonly horizontally; pollen grains finely reticulate, 19–23 μ long, 16–21 μ broad.

Female flower: pedicel c. 0.6–0.75 mm. in anthesis, becoming (1–) 1.2–1.7 (–2) mm. long, terete or somewhat angled, smooth, olivaceous. Calyx-lobes 5 (very rarely 6), obovate-oblong, becoming (0.75–) 0.9–1.1

mm. long and (0.25–) 0.4–0.6 mm. broad, acute, herbaceous with rather broad yellowish-white scarious margins (the green midstrip c. 1/3 the breadth of the calyx-lobe), the midrib unbranched. Disk flat, deeply 5-lobed, sometimes with 1 or more small extra lobes, otherwise entire, not glandular. Styles free, erect or ascending (later becoming more or less spreading), c. 0.1–0.15 mm. long, very shallowly bifid, the lobes blunt.

Capsule oblate, obtusely trigonous, (1.8–) 1.9–2.1 mm. in diameter, smooth, stramineous, the veins almost or completely invisible. Seeds sharply trigonous, light brown, 0.9–1 mm. long, 0.7–0.8 mm. radially and tangentially, with 5 or 6 straight parallel longitudinal ribs on the back (these rarely or never anastomosing), minutely transversely striate with hygroscopic cells which project as hyaline setae with a pronounced notching of the lumen.

Collected flowering and fruiting throughout the year.

Type: Africa, Guinea, Schumacher & Thonning (C, Holotype, not seen; K, type fragment and sketches).

DISTRIBUTION: native to America, now a circumtropical weed. It being impracticable to cite all the specimens examined of this ubiquitous species (which probably occurs on all the islands of the West Indies), only the following representative collections are listed.

BERMUDA: Brown & Britton 369 (F, GH, NY, US). BAHAMAS: Castle Island, Wilson 7802 (F, GH, MO, NY). CUBA: Santiago de las Vegas, Wilson 1075 (F, GH, L, MO, NY, P, US). JAMAICA: Hope Gardens, Harris 12136 (C, F, GH, JAM, NY, P, US). HAITI: Gros Morne, Leonard 9803 (US). DOMINICAN REPUBLIC: Paraíso, Fuertes 1004 (F, GH, NY, P, US). PUERTO RICO: Santurce, Heller 6406 (F, GH, NY, P, US). ST. THOMAS: Wydler 76bis (F, NY). ST. CROIX: Ricksecker 132 (GH, NY, US). ST. MARTIN: Rijgersmaa (S). ST. BARTHELEMY: von Goes (S). GUADE-LOUPE: Duss 2447 (NY). DOMINICA: W. & B. Hodge 3038 (GH). MARTINIQUE: Sieber Herb. Mart. Suppl. 3 (F). ST. VINCENT: Morton 5156 (US). GRENADINES: Carriacou, Howard 10871 (GH). GRENADA: Broadway 4437 (BR). TOBAGO: Broadway 3064 (F, GH, L, P). TRINIDAD: Baker (TRIN 14789).

Although it is doubtless the commonest species in the genus, *P. amarus* has been poorly understood up to the present. Linnaeus initiated much of the confusion by listing Plukenet's reference to *P. amarus* in the synonymy of *P. niruri*, although he filed his only specimen of the former with *P. urinaria* (in the Linnaean Herbarium). Swartz (Obs. Bot. 355. 1791) unfortunately completed the confusion by confounding *P. amarus* and two other species (neither of them Linnaeus's plant!) under "P. niruri" and observing that the Linnaean species appeared to have been introduced into Jamaica from the East Indies. Baillon (Adansonia 2: 18. 1861) definitely regarded *P. niruri* as an "East Indian" species; but his concept, to judge from the specimens he cited, was based on a mixture of *P. amarus* and *P. stipulatus*. Mueller stabilized the situation by equating *P. amarus* with

the typical variety (genuinus) of his polytypic P. niruri, and as a result the specimens of P. amarus from America and Asia have been 100 percent misidentified. Further details of the nomenclatural history have been reviewed previously (Jour. Arnold Arb. 37: 6–8. 1956) and need not be

repeated here.

Although superficially *P. amarus* resembles many other species in sect. *Phyllanthus*, it is taxonomically rather isolated and can always be identified even from fragmentary herbarium specimens. Its best distinguishing feature is the inflorescence of bisexual rather than unisexual cymules; but in addition, the pentamerous calyx with acute lobes, the very short erect styles, and the usually 5-lobed female disk together make it easy (at least with the use of a lens) to distinguish *P. amarus* from such apparently similar plants as *P. stipulatus* or *P. fraternus*. The seeds of *P. amarus*, however, are very similar to those of *P. fraternus*, which in a number of ways appears to be rather closely related to the present species.

The closest relative of P. amarus, however, is undoubtedly P. abnormis Baill. of the southern United States, which is the only other species in the subsection with bisexual cymules. The two resemble one another in so many respects that they are obviously intimately related, although P. abnormis is unquestionably distinct by virtue of its larger capsule, perennial habit, and 4-merous male calyx. This close affinity with P. abnormis is incidentally perhaps the best evidence that P. amarus is a natively American species, which probably originated somewhere in the Caribbean area before it began its highly successful peregrinations in the footsteps

of man.

1866.

21. Phyllanthus stipulatus (Raf.) Webster, Contr. Gray Herb. 176: 53. 1955. (PLATE XIX, figs, L-M).

Phyllanthus niruri sensu Sw. Obs. Bot. 354-355. 1791 (ex p.).

Moeroris stipulata Raf. Sylva Tellur. 91-92. 1838.

Phyllanthus diffusus Klotzsch, Bot. Voy. Herald 105. 1853.

Phyllanthus hoffmannseggii Muell. Arg. Linnaea 32: 45. 1863.

Phyllanthus diffusus a genuinus Muell. Arg. in DC. Prodr. 15(2): 409-410. Phyllanthus aquaticus Wright, Anal. Acad. Ci. Habana 7: 110. 1870.

Diasperus diffusus (Kl. "em.") O. Ktze. Rev. Gen. 2: 599. 1891.

Erect annual herb, usually with a single sparsely to copiously branching main stem 2–5 (–10) dm. high and 1–2 (–4) mm. thick, sometimes spongy or bladdery at base (when plant grows in water), above light brown, smooth, terete; internodes (0.5–) 1.5–5 (–6) cm. long. Cataphylls: stipules triangular, (0.6–) 0.7–1 mm. long, (0.3–) 0.4–0.6 mm. broad, acuminate, not auriculate at base (or at most obscurely so), entire, light reddish-brown becoming darker, but remaining thin and scarious; blade linear-lanceolate, acuminate, 0.5–0.9 mm. long, 0.1–0.3 mm. broad. Deciduous branchlets (1–) 2–6 (–9) cm. long, light brown, often reddish-

tinged, smooth or scabridulous, more or less terete, with (12–) 15–30 (–35) leaves; first internode 2.5–13 mm. long, internodes between male flowers 1–2.7 mm. long, between female flowers 1.3–3 mm. long. Leaves: stipules lanceolate, (0.5–) 0.7–1 mm. long, (0.1–) 0.2–0.3 mm. broad, acuminate-attenuate, entire, reddish-brown, scarious. Petioles 0.4–0.6 mm. long. Leaf-blades membranous to chartaceous, smooth or minutely scabridulous on one or both sides, mostly oblong-elliptic but sometimes ovate or suborbicular, (2.5–) 3–10 (–13) mm. long, 2–4 (–6) mm. broad, obtuse or rounded to nearly truncate at the tip, obtuse or rounded at the base, not oblique or scarcely so; above bright green, midrib raised in lower half, running obscurely to the tip, the laterals obscure; beneath pale, the midrib raised, the laterals (4–6 on a side) rather conspicuous, the reticulum of tertiary veinlets evident to obscure; margins smooth, not especially thickened, often reddish-tinged.

Monoecious; proximal (0-) 2-8 axils barren; succeeding (2-) 3-7 (-9) axils with monochasial cymules of 3-5 (-10) male flowers; distal axils with solitary female flowers.

Male flower: pedicel 0.4–0.7 mm. long. Calyx-lobes 5 (rarely 4 or 6), obovate or broadly elliptic to orbicular, (0.5-) 0.6–0.9 mm. long and about as broad, rounded at the tip, entire, pale yellowish, scarious except for the unbranched midrib. Disk-segments 5 (rarely 6), elliptic to orbicular, entire or crenulate-lobate, sometimes conspicuously glandular, c. 0.1–0.2 mm. across. Stamens 3 (rarely 2); filaments completely connate into a column c. 0.25–0.35 mm. high; anthers sessile atop the column, ascending, c. 0.2–0.25 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 20–24 μ long, 17–21 μ broad.

Female flower: pedicel becoming 1.5–2.5 mm. long, olivaceous, minutely scabridulous or nearly smooth, terete below, somewhat angular above. Calyx-lobes 5, obovate, in flower c. 0.8–1.2 mm. long, in fruit becoming (1.2–) 1.4–1.8 (–2) mm. long and 0.8–1.3 (–1.5) mm. broad, obtuse or rounded at the tip, olivaceous with broad whitish scarious margins, the more or less dorsally carinate midrib unbranched. Disk patelliform and obscurely 5-angled or variously lobed, sometimes markedly asymmetric. Styles separate, ascending or spreading, 0.2–0.3 mm. long, bifid, the branches recurved, subcapitate at the tips.

Capsule c. 2.4–2.5 mm. in diameter, obscurely rugulose above, stramineous, the veins completely obscure. Seeds sharply trigonous, 1.1–1.3 mm. long, 0.8–0.9 mm. radially and tangentially, light brown, with c. 10–12 subpaired very delicate longitudinal striae (these often completely obscure), transversely banded with clavate hygroscopic epidermal cells.

Collected throughout the year.

Type: Jamaica, Swartz (S, Holotype). The typification of this species, which formed a portion of Swartz's concept of *P. niruri*, has been discussed in detail elsewhere (Jour. Arnold Arb. 37: 9. 1956).

DISTRIBUTION: widespread in tropical America, usually in moist habitats and sometimes growing in shallow water (MAP IX).

CUBA. PINAR DEL Río: Pinar del Río City, road to Matea Sanchez, Ekman 17855 (NY, S); Santa Cruz de los Pinos, in savannas, Ekman 17696 (S); "a la orilla de lagunas cerca de Pinar del Río" [ex Sauvalle], Wright 3683 (F, GH, NY, P, S, US); type collection of P. aquaticus Wright). Isla de Pinos: Santa Barbara, Westport, Ekman 12070 (S); road to San Francisco de las Piedras, Killip 45238 (GH); Salta Mamey, Killip 45276 (GH); San Pedro and vicinity, Britton & Wilson 15437 (F, MO, NY, US).

JAMAICA: without exact locality, Swartz (S, Holotype). St. Elizabeth: Cornwall, shallow water in pond, Harris 12555 (GH, JAM, MO, NY, US). Clarendon: Hollis's Savanna, 2,400 ft. alt., Harris 12224 (F, NY, P). St. Catherine: boggy pond, 2 miles southwest of Ewarton, Proctor 6177 (A).

HAITI. ARTIBONITE: St.-Michel de l'Atalaye, savannas toward Maissade, Ekman H9406 (S).

DOMINICAN REPUBLIC. Samaná: Peninsula Samaná, Samaná, road to Río San Juan, Ekman H14836 (S); Peninsula Samaná, Sanchez, along the railroad in the Gran Estero, Ekman H14721 (S). La Vega: Loma del Oro, cerca de Hatillo, alt. 240 m., Jiménez 2697 (US). Trujillo: Villa Altagracia, Ekman H11220 (A, S); savanna land between Bayaguana and Guerra, R. A. & E. S. Howard 9895 (GH). Santo Domingo: Llano Costero, Cuenca, Ekman H10093 (S).

PUERTO RICO: without specific locality, Ridley (G), Herb. Ventenat (G). AGUADILLA: near Lares, Underwood & Griggs (NY). Guayama: mountain between Guayama and Cayey, alt. 700–900 m., Britton, Britton, & Brown 6359 (NY). Mayaguez: Cabo Rojo, Sintenis 775 ex p. (GH); Mayaguez, Stevens 2516 (NY). San Juan: Luquillo, Bayamon, Otero 523 (A, MO); University Farm, Río Piedras, Dale (MICH); near Bayamon, Underwood & Griggs 874 (NY).

LESSER ANTILLES. Montserrat: near the lake of the mountains, alt. c. 1200 ft., Shafer 179 (NY). Guadeloupe: Dugommier (Gourbeyre), Stehlé 1028 (NY); Basse-Terre, Duss 214 (P); Plonel, Rodriguez 3896 (P). Martinique: Saint-Pierre, Parnasse, Macouba, Marigot, Duss 46 (NY); quartier du Lamentin, Plée (P). St. Vincent: 1826, Parker (P). Trinidad: without locality, Finlay (TRIN 2462); Piarco Savanna, Baker (TRIN 14855), Warming 829 (C), H. Wright P-10 (TRIN).

Phyllanthus stipulatus is a plant of predominantly moist habitats, and it often grows in shallow water in swamps, where it may develop aerenchyma prominently at the base of the stem. Its relatively narrow habitat preference explains the spottiness of its distribution as compared to the more nearly ubiquitous P. amarus of this same subsection. It has often been confused with P. niruri and P. amarus; but the first may be easily distinguished by its inequilateral leaves, narrower stipules, and verruculose seeds, while the latter is always recognizable by its bisexual cymules and narrower acute calyx-lobes. The species in the West Indies most closely related to P. stipulatus is undoubtedly P. caribaeus, which, however, differs in its partially united filaments and peculiar female disk.

Phyllanthus microphyllus H.B.K., of South America, is also similar but

differs among other respects in being dioecious.

It is interesting that one of the species most similar to *P. stipulatus* is *P. nigericus* Brenan, recently (Kew Bull. 1950: 215) described from tropical West Africa. This species, to judge from the description, is exceedingly similar to *P. stipulatus* in almost all morphological details except for its 9-lobed female disk and longer fruiting calyx-lobes. Its habitat preference, as cited for the type collection, is also like that of *P. stipulatus*. This close relationship between an American and African species, which is paralleled elsewhere in sect. *Phyllanthus*, presents an interesting and as yet unelucidated phytogeographic problem.

In contrast to such wide-ranging American species as *P. caroliniensis* and *P. niruri*, *P. stipulatus* exhibits little, if any, geographic variation. The variations which do occur, such as the production of 2 stamens instead of 3 or nearly orbicular leaves instead of elliptical ones, appear to have a purely random distribution throughout the range of the species. Mueller (DC. Prodr. 15[2]: 410. 1866) distinguished a narrow-leaved var. *oblongifolius*, from South America, but this appears to be specifically distinct and identical with the plant he later (Fl. Bras. 11[2]: 54. 1873) described as *P. minutulus*. It seems unlikely that any subspecific entities

will ever be distinguished within P. stipulatus.

22. Phyllanthus caribaeus Urb. Symb. Ant. 5: 382-383. 1908. (PLATE XIX, figs. N-O).

Slender erect annual herb; primary stem simple, 1-3.5 dm. high, 0.5-2 mm. thick, stramineous or pale brown, smooth, terete; internodes mostly 2-4 cm. long. Cataphylls: stipules lanceolate, mostly 0.6-0.9 mm. long and 0.3-0.35 mm. broad, acuminate, scarious, entire, not auriculate at base, reddish-brown; blade linear-lanceolate, 0.5-0.8 mm. long. Deciduous branchlets (2-) 3-7 cm. long, 0.15-0.25 (-0.3) mm. thick, light brown, smooth or minutely scabridulous, terete or obtusely angled, with mostly 15-30 leaves; first internode 5-12 (-15) mm. long, median internodes 1-2 (-2.5) mm. long. Leaves: stipules lanceolate, (0.5-) 0.7-0.8 (-1) mm. long, c. 0.2-0.25 mm. broad, attenuate-acuminate, entire, reddishbrown with very narrow whitish edges, scarious. Petioles 0.3-0.4 mm. long. Leaf-blades membranous, minutely scabridulous on both sides, mostly ovate-oblong but sometimes elliptic (usually narrowed from below the middle to the tip), 4-8 mm. long, 2-3.3 mm. broad, obtuse at the tip, obtuse or truncate-rounded at the base; above bright green, the nerves rather obscure; beneath paler, the midrib prominent, the laterals (c. 4 or 5 on a side) quite evident, the tertiary veinlets forming a delicate reticulum; margins smooth or minutely roughened, scarcely if at all thickened, plane, sometimes reddish-tinged.

Monoecious; proximal (2-) 3-7 (-9) nodes barren, succeeding 4-6 (-8) nodes with bracteolate cymules of up to 4 or 5 successively maturing male flowers, distal nodes with solitary female flowers.

Male flower: pedicel c. 0.3–0.8 mm. long. Calyx-lobes 5, suborbicular or broader than long, 0.4–0.5 mm. long, 0.4–0.6 mm. broad, obtusely rounded to nearly truncate at the tip, entire, membranous, yellowish-white, the midrib unbranched. Disk-segments 5, cuneate or nearly round, 0.15–0.2 mm. across, glandular-crenate. Stamens 3, filaments c. 0.2–0.25 mm. long, united in the lower half into a slender column; anthers c. 0.1–0.15 mm. long, 0.15–0.2 mm. broad; anther-sacs divaricate, the slits apically confluent, dehiscing horizontally or nearly so; pollen grains finely reticulate, 20–22 μ long, 17–20 μ broad.

Female flower: pedicel becoming 1.5–2 mm. long, stramineous, minutely scabridulous or nearly smooth, terete below, angular and broader above. Calyx-lobes 5, oblong to obovate, somewhat unequal, c. 1–1.2 mm. long at anthesis, becoming 1.2–1.4 (–1.6) mm. long and 0.6–0.9 mm. broad in fruit, obtuse at the tip, entire, olivaceous in the middle with very broad whitish scarious margins, the midrib not evidently branched. Disk dissected into 3 erect narrowly linear somewhat unequal segments (the largest one often bifid or rarely double) c. 0.3–0.5 mm. long, these later spreading. Styles free, spreading or ascending, c. 0.25 mm. long, bifid, the branches spreading, the tips slightly thickened.

Capsule c. 2 mm. in diameter, stramineous, obscurely rugulose above, the veins completely obscure. Seeds yellowish-brown, 0.9–0.95 mm. long, 0.7–0.75 mm. radially and tangentially, with c. 10 very delicate longitudinal striae and many fine transverse bars.

Collected in flower and fruit September through March.

Type: Tobago, Eggers 5733 (F, Lectotype; NY, Isotype). This Eggers collection is hereby designated as the lectotype, since Urban failed to make any distinction among the six collections he cited.

DISTRIBUTION: apparently endemic to the Lesser Antilles and Trinidad, but possibly to be discovered in South America (MAP IX).

LESSER ANTILLES. Dominica: Lisdara, pastureland weed, *Hodge 2425* (GH). St. Vincent: open places, fields, &c., *H. H. & G. W. Smith 515* ex p. (NY, mixed with *P. amarus*). Grenada: banks of the main road, Animas, *Broadway* (F; NY, mixed with *P. urinaria*); cultivated ground, Grenville, *Hunnewell 19477* (GH). Tobago: Cradley, *Eggers 5733* (F, Lectotype; NY, Isotype); northside road, King's Bay to Charlotteville, *Freeman & Williams* (TRIN 11387).

TRINIDAD: without specific locality, Wullschlaegel 1073 ex p. (W, mixed with P. stipulatus); Aripo Savanna, Broadway 6489 (M, T, NY); Cascade, St. Ann's, on banks in shade, Broadway 5124 (F, G, MO, NY); Long Stretch, Broadway 6545 (MO, S); Maracas, road to the bay, south, Broadway 6756 (F, MO, S); Morne Bleu, Arima, Freeman (TRIN 9566).

This species is closely related to P. stipulatus and at first glance may appear to be merely a slender form of that species. The leaves, however, tend to be more pointed, tapering the entire length from base to apex, whereas they are usually elliptic or oblong in P. stipulatus. Furthermore,

P. caribaeus is well distinguished by its only partially connate filaments, peculiar female disk, and smaller seeds. Consequently, there can be little doubt that P. caribaeus merits specific rank despite its obviously very near relationship to P. stipulatus. It would be of considerable interest to study the two species in the field in St. Vincent or Trinidad, where they occur sympatrically, to determine what differences — if any — they show in habitat preference.

23. Phyllanthus procerus Wright, Anal. Acad. Ci. Habana 7: 149. 1870. (PLATE XIX, figs, P-R).

Slender to robust annual herb, usually with a single subsimple primary stem 1-7.5 dm. high, 0.5-1.5 mm. thick, light brown, smooth, terete, slightly channeled; internodes 1-9 cm. long (usually at least one or more as much as 2.5 cm. long). Cataphylls: stipules ovate-triangular, 0.6-1.5 mm. long, 0.4-0.8 mm. broad, acuminate, truncate or with a small usually poorly developed auricle at base, entire or obscurely toothed, pale pinkishbrown becoming reddish or dark brown, remaining scarious (never blackish and indurate); blade linear-lanceolate, acuminate, 0.5-1 mm. long. Deciduous branchlets (3-) 5-15 (-20) cm. long, 0.3-0.45 mm. thick, olivaceous, smooth, terete or obscurely angled, with (20-) 30-60 leaves; first internode (2-) 3.5-11 mm. long, median internodes 1-3 mm. long. Leaves: stipules narrowly ovate-lanceolate, 0.5-1 mm. long, 0.15-0.3 mm. broad, acuminate, entire, brownish or pinkish with narrow whitish or yellowish margins. Petioles 0.2-0.4 mm. long. Leaf-blades membranous, linear to narrowly elliptic or ovate-oblong, (3-) 4-7 mm. long, 1-1.8 mm. broad, obtuse or rounded and more or less apiculate at the tip, obtuse at the base; above olivaceous, smooth, the midrib plane, the laterals completely obscure; beneath paler, smooth, the midrib proximally raised, the laterals (4 or 5 on a side) inconspicuous or obsolete; margins slightly thickened, smooth or obscurely roughened, sometimes slightly reddish-tinged.

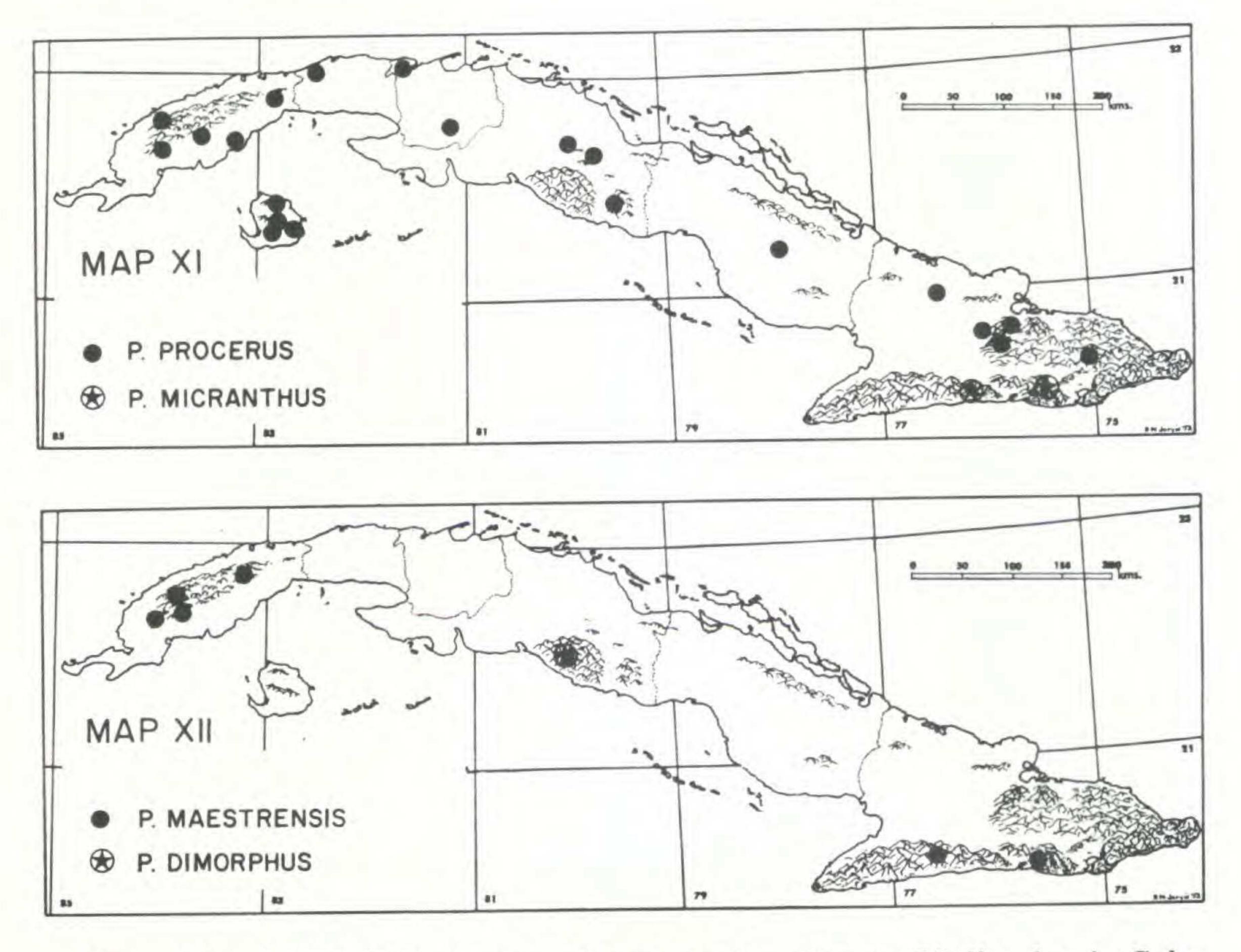
Monoecious; proximal (0-) 4-18 (-30) nodes barren; succeeding (3-) 10-25 (-36) with racemiform cymules of 3-8 male flowers, the cymule axis c. 0.5 mm. (rarely to 0.75 mm.) long; distal nodes with solitary female flowers.

Male flower: pedicel 0.3–0.8 mm. long. Calyx-lobes 5, subequal, sub-orbicular to broadly obovate or obcordate, often broader than long, c. 0.5–0.7 mm. long and broad, rounded or emarginate at the tip, yellowish-white, the median area poorly demarcated from the broad scarious subhyaline margins, the midrib unbranched. Disk-segments 5, cuneate to orbicular, 0.15–0.2 mm. across, smooth, entire, not evidently glandular. Stamens usually 2, occasionally 3 but then the third anther usually reduced; filaments completely united into a column 0.2–0.25 mm. high; anthers sessile atop the column, more or less fused back-to-back by the connectives, c. 0.15–0.2 mm. long, 0.3–0.4 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits apically confluent (and the slits of both anthers

sometimes becoming confluent); pollen grains finely reticulate, 28–32 μ long, 25–27 μ broad.

Female flower: pedicel becoming 1.2–1.8 (–2) long, olivaceous, smooth, subterete, gradually dilated from the base upwards. Calyx-lobes 5, ovate to suborbicular at anthesis, in fruit becoming elliptic or obovate and 0.75–1 mm. long, 0.7–1 mm. broad, obtuse or rounded at the tip (sometimes acute in fruit), olivaceous with usually broad whitish scarious margins, the midrib unbranched. Disk obtusely (or less commonly, acutely) shallowly or deeply 5-lobed, smooth, rather thin. Styles free, horizontal or somewhat ascending, c. 0.15 mm. long, bifid c. ½ their length, the branches bent at a right angle and unequally thickened so that each style resembles the arm of a Maltese cross.

Capsule oblate, 2.3-2.5 mm. in diameter, light yellowish-brown, obscurely rugulose at the top, the veins not visible. Seeds (1.1-) 1.2-1.3



Maps XI and XII. Distribution of some species of sect. Phyllanthus in Cuba.

(-1.35) mm. long, 0.9–1.05 mm. radially, 0.8–1.05 mm. tangentially, fuscous (when mature), with c. 11–13 very tenuous subpaired longitudinal striae and many transverse striae (of not or scarcely hygroscopic cells) on the back, the intersections of longitudinal and transverse striae often darkened to give a banded effect.

Collected in flower and fruit throughout the year.

Type: Cuba, Pinar del Río, Wright 3684 ex p. (GH, LECTOTYPE; NY,

P, S, US, ISOTYPES). This collection consists of a mixture of *P. procerus* and *P. maestrensis*. However, since Wright's description of the flowers clearly does not apply to the latter element, which has introrse anthers, the name *P. procerus* must be associated with the other plant, which has been described above.

DISTRIBUTION: endemic to Cuba, usually occurring in savannas (MAP XI).

CUBA. PINAR DEL Río: Baños San Vicente, Britton et al. 7483 (NY); among tall grasses in thickets surrounded by pine woods, Pinar del Río, Wright 3684 (GH, LECTOTYPE; NY, P, S, US, ISOTYPES; data ex S); Colpothrinax savanna, Herradura, Britton et al. 6465 (NY); Herradura to Paso Real, savanna, Shafer 11747 (NY); San Gabriel to Pinal de la Catalina, sandy pineland, Shafer 11852 (MO, NY); between Candelaria and Artemisa, Wilson 1733 (NY); San Isidro, along arroyo, Britton et al. 13961 (NY). Isla de Pinos: sabanas between Santa Barbara and Mina de Oro, Killip 42789 (US); sabanas, Nueva Gerona, Curtiss (NY), Killip 42547 (US); Nueva Gerona, Loma Vista, Ekman 12372 (S); ditch along road, San Francisco de las Piedras, Killip 42789 (US); fields, Finca Mamey, headwaters of Río Casas, Killip 44705 (US); woods at base of Sierra de Caballos, near Presidio, Killip 44534 (US); San Pedro, river woods, Britton et al. 14457 (NY); sabanas near southeast corner of Cerro Daguilla, Killip 43952 (US); field near pond, San Juan, Killip 45332 (GH). HABANA: Punta Brava, Baker & O'Donovan 3999 (NY). MATANZAS: Tetas de Camarioca, serpentine barren, Britton et al. 14059 (NY, US); Jaguey Grande, pastures, Ekman 16967 (S). Las Villas: serpentine barrens near Santa Clara, Britton et al. 6114 (F, NY), Webster 4173 (GH, MICH); Lomas de Banao, Luna 90 (NY); Placetas del Sur, palm barren, Leon & Roca 8163 (NY); wet savannas, La Sierpe, south of Sancti Spiritus, Alain 1562 (MICH). Camaguey: savannas near Camaguey, Britton et al. 13127 (NY). ORIENTE: roadside 8 km. west of Holguin, Jervis 1961 (MICH); savanna, Hato del Medio, 23 Aug. 1860, Wright 1936 (GH); Sierra de Nipe, Pinar de Mayarí, Carabia 3807 (NY); in charrascales prope Río Pilote, Ekman 2164 (S); open grass-covered places in pinelands near Río Piedra, Ekman 1835 (S); open pines near Bandera trail, Shafer 3245 (NY); San Andrés near Monte Verde, margin of rivulets, Wright (W., probably Wright 1675); banks of Pinal Creek, Monte Verde, Wright 1675 ex p. (GH); without definite locality, Wright "420" (GOET), Wright (S; these two collections representing either Wright 1936 or 1675).

This common species of savannas throughout Cuba is doubtlessly closely related to *P. micranthus*, to which it has been referred by Urban (Repert. Sp. Nov. 13: 452. 1914) and Alain (Fl. Cuba 3: 58. 1953). However, it appears to be sufficiently distinct by virtue of its peculiar stylar configuration and its smaller and broader male calyx-lobes. The anthers are definitely connate at their bases in *P. procerus*, and occasionally the slits of the two anthers become confluent so that the androecium approaches the synandrial condition of *P. dimorphus*; in *P. micranthus*, on the other hand, the anthers are discrete.

Also related to P. procerus is P. maestrensis, which unlike P. micranthus has a sympatric distribution in Pinar del Río; it has already been noted that Wright himself apparently gathered the two species together when he

made the type collection of *P. procerus*. *Phyllanthus maestrensis* differs from *P. procerus* in its larger male flowers with introrse stamens, larger leaves, and indurate cataphyllary stipules.

24. Phyllanthus fadyenii Urb. Symb. Ant. 6: 13. 1909; Fawc. & Rend. Fl. Jam. 4:255. 1920. (PLATE XXII, fig. A).

Phyllanthus orbicularis sensu Griseb. Fl. Br. W. Ind. 34. 1859; non P. orbicularis H. B. K.

Apparently a subshrub or woody herb, glabrous; branches terete, 1-3 mm. thick, furrowed, smooth, or the bark somewhat cracking, greyish or dark brown. Cataphylls: stipules lanceolate, 1.5-1.8 mm. long, 0.6-0.7 mm. broad, acuminate, entire, not auriculate at the base, dark reddishbrown, becoming more or less persistent; blade linear-lanceolate, 1-1.5 mm. long, less than 0.3 mm. broad, acuminate. Deciduous branchlets (0.5-) 1-1.5 cm. long, 0.25-0.3 mm. thick, terete, smooth, reddish-brown, with (7-) 10-15 nodes; first internode c. 1.5-2.5 mm. long, median internodes 0.5-1.2 mm. long. Leaves: stipules linear-lanceolate, those of each pair slightly unequal, 1.1-1.3 mm. long, 0.2-0.3 mm. broad, acuminate (or sometimes bluntish), reddish-brown, firm, persistent. Petiole 0.2-0.3 (-0.4) mm. long. Leaf-blades firm but hardly coriaceous, broadly oblong or ovate, 4-5.5 mm. long, 2.5-4 mm. broad, rounded or obtuse at the tip, emarginate-cordate at the base; above olivaceous, the midrib plane, the laterals obsolete or invisible; beneath brownish, the midrib scarcely raised, the laterals (c. 4 or 5 on a side) conspicuous, straight, only slightly anastomosing; margins somewhat thickened, deeply reddishtinged, plane.

Monoecious; flowers apparently solitary or paired, the male and female flowers at separate axils.

Male flower: pedicel less than 1 mm. long. Calyx-lobes 5, subequal, broadly obovate or suborbicular, 0.7–0.8 [–1.2, ex Urban] mm. long, 0.6–0.9 mm. broad, the midrib unbranched. Disk-segments 5, reniform, smooth, entire, c. 0.2 mm. broad. Stamens 3; filaments free, becoming 0.5 mm. long (Urban); anthers erect, 0.3–0.4 mm. long, 0.4–0.5 mm. broad; anther-sacs divergent, opening longitudinally.

Female flower: pedicel 3–3.5 mm. long. Calyx-lobes 5, subequal, sub-orbicular or broadly elliptic in fruit, 1.7–2 mm. long, 1.4–1.7 mm. broad, rounded at the tip, entire, herbaceous with narrow and inconspicuous pale scarious margins, the midrib unbranched. Disk shallowly cupuliform, thin, the rim undulate. Ovary smooth, subglobose; styles coherent at the base, spreading, 0.2 mm. long, bifid, the branches reflexed with thickened subcapitate tips.

Capsule and seeds not seen; persistent columella 0.7 mm. long.

Type: Jamaica, McFadyen (K, HOLOTYPE).

DISTRIBUTION: known only from the type collection.

Although this plant is still incompletely known, there is little doubt that it belongs in sect. *Phyllanthus*; as Urban pointed out, it has nothing more in common with *P. orbicularis* (sect. *Orbicularia*) than a superficially similar aspect. However, the place of *P. faydenii* within subsect. *Swartziani* is very doubtful, for its woody stems and free stamens do not accord with the subsectional character. When pollen grains and seeds of *P. fadyenii* become available, it may be possible to assign it to a more definite position. For the present, it is kept in subsect. *Swartziani* because of its non-auriculate stipules, but it should be noted that in aspect it resembles such species of subsect. *Pentaphylli* as *P. selbyi* and may ultimately prove to belong to that subsection.

Subsect. 11c. Pentaphylli Webster, Contr. Gray Herb. 176: 54. 1955.

Annual or perennial herbs, sometimes woody at the base; cataphyllary stipules conspicuously auriculate at the base, usually blackened and indurate; leaves equilateral at base; branchlet stipules not involute; monoecious or dioecious, cymules unisexual; calyx-lobes 5 or 6; stamens 2 or 3, filaments partially to wholly united, pollen grains 3-colporate, finely or coarsely reticulate; female disk patelliform or variously lobed or divided; styles free, deeply to shallowly bifid, the tips not capitate; seeds finely longitudinally striate or banded and transversely striate or barred.

Type species: Phyllanthus pentaphyllus Wright.

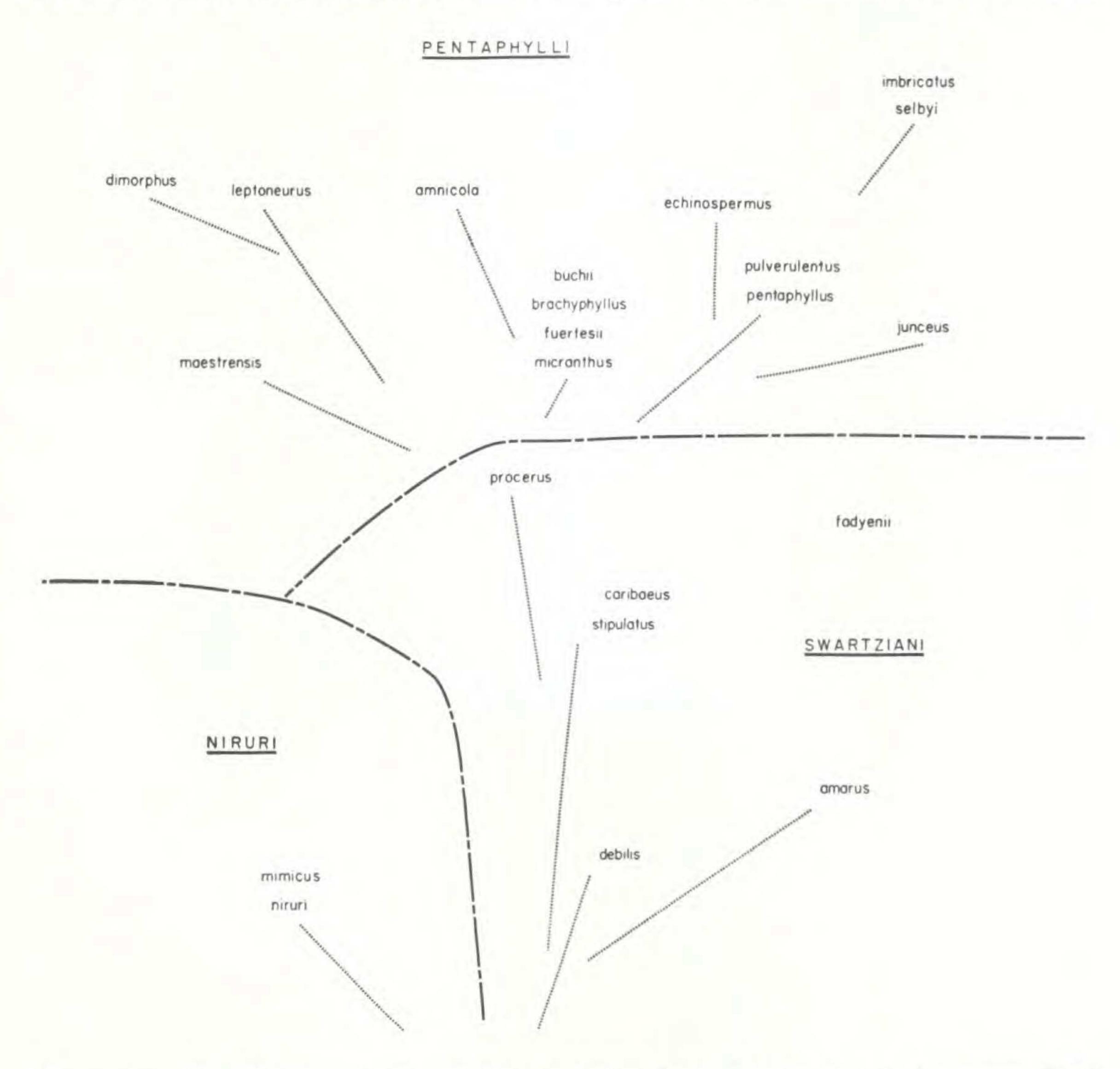
Subsect. *Pentaphylli*, which appears to be essentially endemic to the West Indies, shares with sect. *Orbicularia* the distinction of having the largest number of endemic West Indian species and subspecies. As might be expected, its component species show adaptive radiation to a considerable variety of habitats, such as white sands along lagoons (*P. echinospermus*), savannas (*P. junceus*), coral platforms near the sea-coast (*P. pentaphyllus*), grassy hillsides (*P. dimorphus*), and stream-beds (*P. maestrensis*).

The variation in the male flowers — particularly with regard to the androecium — within this subsection is remarkably large; and on the basis of purely formal morphology, such species as *P. dimorphus* (with a synandrium like that of sect. *Cyclanthera*) and *P. maestrensis* (with unique introrse anthers) could be placed in special monotypic subsections. However, both of these species are manifestly rather closely related to species with conventional androecia.

The Cuban species of subsect. *Pentaphylli* are on the whole well-defined and not difficult to classify, but the situation is very different with regard to the species in Hispaniola. Here the species complex comprising *P. brachyphyllus*, *P. buchii*, and *P. fuertesii* has proved to be completely intractable to systematic analysis; these species cannot be satisfactorily demarcated from one another nor from *P. micranthus* of eastern Cuba. The numbers of stamens and calyx-lobes, which elsewhere are useful taxonomic characters, are here so variable that it is impossible to devise a

really satisfactory key, even for the relatively few available specimens. Studies of leaf anatomy (including measurement of stomatal size) based on leaves cleared and stained in safranin or haematoxylin have yielded no conclusive results.

Examination of pollen grains has shown an unexpected distinction between *P. dimorphus* and *P. leptoneurus*, which have coarsely reticulate grains unique in sect. *Phyllanthus*, and the remaining species of the subsection, which have the finely reticulate grains of subsect. *Swartziani*. But



Text-fig. 11. Diagrams of putative relationships within the indigenous West Indian species of sect. *Phyllanthus*. The three subsections are separated by black lines, while the apparent lineages of affinity are indicated by broken lines. The degree of relationship is roughly indicated by the distance between the different entities.

within the *P. micranthus* complex, pollen studies have not been particularly rewarding. At first it was hoped that the presumed hybrid or intermediate nature of certain specimens could be confirmed by determination of the percentage of good pollen; but the results have been both puzzling and disappointing, for some presumptive hybrids proved to have apparently good

pollen, while some specimens which appeared to represent "pure" species yielded a large percentage of defective pollen. Thus, although there remains in many cases, a strong presumption of the hybrid nature of some collections, no decisive confirmation is forthcoming from examination of the pollen. The present treatment of the species of the *P. micranthus* complex is admittedly the least satisfactory portion of this entire study; but the problem appears to be insoluble on the basis of the herbarium material at hand and can probably be resolved only by laborious field study, including cytological analysis of the populations from which mongrel or dubious specimens have been collected.

In fortunate contrast to the obscure situation in the Hispaniolan species, the general phylogenetic relationships of subsect. Pentaphylli are rather more clear. It is quite evident that the subsection represents a local Antillean development from some ancestral form in subsect. Swartziani; and in fact P. procerus, certainly, and P. fadyenii, probably, may be considered directly related to the members of subsect. Pentaphylli. Phyllanthus procerus, indeed, resembles P. micranthus so closely that it has usually been combined with that species; but it clearly belongs in subsect. Swartziani because of its non-indurate, scarcely (if at all) auriculate cataphyllary stipules. It would thus appear that in passing from P. procerus to P. micranthus we have traced the origin of subsect. Pentaphylli, but — as is so often the case—the matter is not quite so simple as that. Phyllanthus procerus is highly specialized in a number of respects, particularly in its reduced androecium of two stamens and its peculiarly modified styles; it is therefore necessary to postulate some less highly modified species as the ancestor of subsect. Pentaphylli. Phyllanthus fadyenii, with its androecium of three free stamens and less highly specialized styles, may prove to be closer to the prototype, but its affinity must remain doubtful until its seeds and pollen grains can be studied.

The graphical arrangement of presumed species relationships (Text-fig. 11) is intended only to point out lines of affiliation but not to convey the impression that some species are any more "highly evolved" than others. Thus *P. procerus*, although placed at the base of the lines leading to the species of subsect. *Pentaphylli*, is not to be regarded as the ancestor of that subsection, but rather as the closest living relative of that ancestral form.

Phyllanthus micranthus A. Rich. Hist. Nat. Cuba 11: 216. 1850;
 Muell. Arg. in DC. Prodr. 15(2):412. 1866. (PLATE XX, fig. A).

Diasperus micranthus (A. Rich.) O. Ktze. Rev. Gen. 2: 600. 1891.

Perennial herb, suffruticose at the base, with few to several erect sparsely branched wand-like stems c. 3–6 dm. high; stems terete, smooth, silvery or brownish; internodes mostly 3–7 (–11) cm. long, 1–1.5 mm. thick. Cataphylls: stipules triangular-ovate, (0.6–) 1–1.4 mm. long, 0.5–0.7 mm. broad, acuminate, entire or basally dentate, conspicuously auriculate, reddish and scarious becoming darker and rigid or reddish-black and indurate

from the first; blade linear-lanceolate, 0.5–0.9 mm. long. Deciduous branchlets (3.5–) 5–13 (–35) cm. long, 0.15–0.3 mm. thick, subterete or obtusely angled, smooth, brownish, with 25–50 (–75) leaves; first internode 4–7 mm. long, median internodes 2.5–4.5 mm. long. Leaves: stipules subpersistent, narrowly lanceolate, 0.6–0.9 mm. long, 0.2–0.3 mm. broad, acuminate, somewhat dilated basally, olivaceous becoming reddish, entire. Petioles 0.3–0.5 mm. long. Leaf-blades membranous, linear-oblong, 4–7 mm. long, 1.2–1.7 mm. broad, acute to obtuse-apiculate at the tip, acute to obtuse at the base; above dark green, the midrib somewhat raised above and below, the laterals obsolete on both sides, pale beneath; margins unthickened, plane, more or less smooth.

Dioecious; first (0-) 2-4 (-8) nodes of male branches barren, succeeding nodes with racemiform cymules of 3-5 male flowers; female flowers

solitary.

Male flower: pedicel 0.6–1.1 mm. long. Calyx-lobes 5, obovate or spathulate, 1–1.2 mm. long, 0.7–1 mm. broad, broadly rounded to emarginate at the tip, entire, with broad scarious margins, the midrib unbranched. Disk-segments 5, elliptic or orbicular, 0.2–0.3 mm. across, entire, flattened, not glandular. Stamens 2 or sometimes (usually in the first flower of a cymule) 3; filaments connate their entire length into a column c. 0.5 mm. long, c. 0.15–0.2 mm. broad; anthers subsessile, discrete, 0.2–0.25 mm. long, 0.25–0.35 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; the pollen grains finely reticulate, 20–22 μ long, 17–18 μ broad.

Female flower: Calyx-lobes 5, oblong-obovate, c. 1.5–1.8 mm. long, rounded at the tip, entire, with rather narrow whitish scarious margins. Disk shallowly 5-lobed, the lobes thin and flat. Styles free, ascending, c. 0.5 mm. long, bifid c. ½ their length, the branches spreading, subcapitate

at the tips.

Fruit and seeds unknown.

Type: Cuba, Linden 2074.

DISTRIBUTION: endemic to eastern Cuba (MAP XI).

CUBA. ORIENTE: St. Yago de Cuba, Pinal de Nimanima, alt. 400 ft., August 1844, Linden 2074 (G, LECTOTYPE; BR, G, P, ISOTYPES; A, type fragment); pinelands, vicinity of El Cuero, alt. 400 m., 18–19 Mar. 1912, Britton & Cowell 12781 (NY).

This species, still imperfectly known, requires further study before its circumscription can be exactly defined. Not only are the capsules and seeds unknown, but female flowers have been observed only on the sheet of Linden's collection in the Prodromus Herbarium, and the notes taken on that specimen are incomplete in some details. It is not surprising that *P. micranthus* has been confused with other species, mainly with *P. procerus*; it does appear to be rather closely related to that species but clearly differs in its perennial growth, dioecious inflorescence, larger spathulate male

calyx-lobes, and discrete anthers. Furthermore, *P. procerus* does not have indurate auriculate cataphyllary stipules and thus must be excluded from subsect. *Pentaphylli*. However, *P. micranthus* is also closely related to two Hispaniolan species, *P. fuertesii* and *P. brachyphyllus*. These differ in having usually 6-merous calyces and 3 stamens, as well as broader leaves. Previously (Contr. Gray Herb. 176: 55. 1955) it was suggested that *P. fuertesii* represented only a subspecies of *P. micranthus*. There still is no question of its very close relationship, but until the Hispaniolan species are better understood it seems preferable not to combine them with *P. micranthus*.

26. Phyllanthus fuertesii Urb. Repert. Sp. Nov. 13: 451-452. 1914. (PLATE XX, figs. B-C).

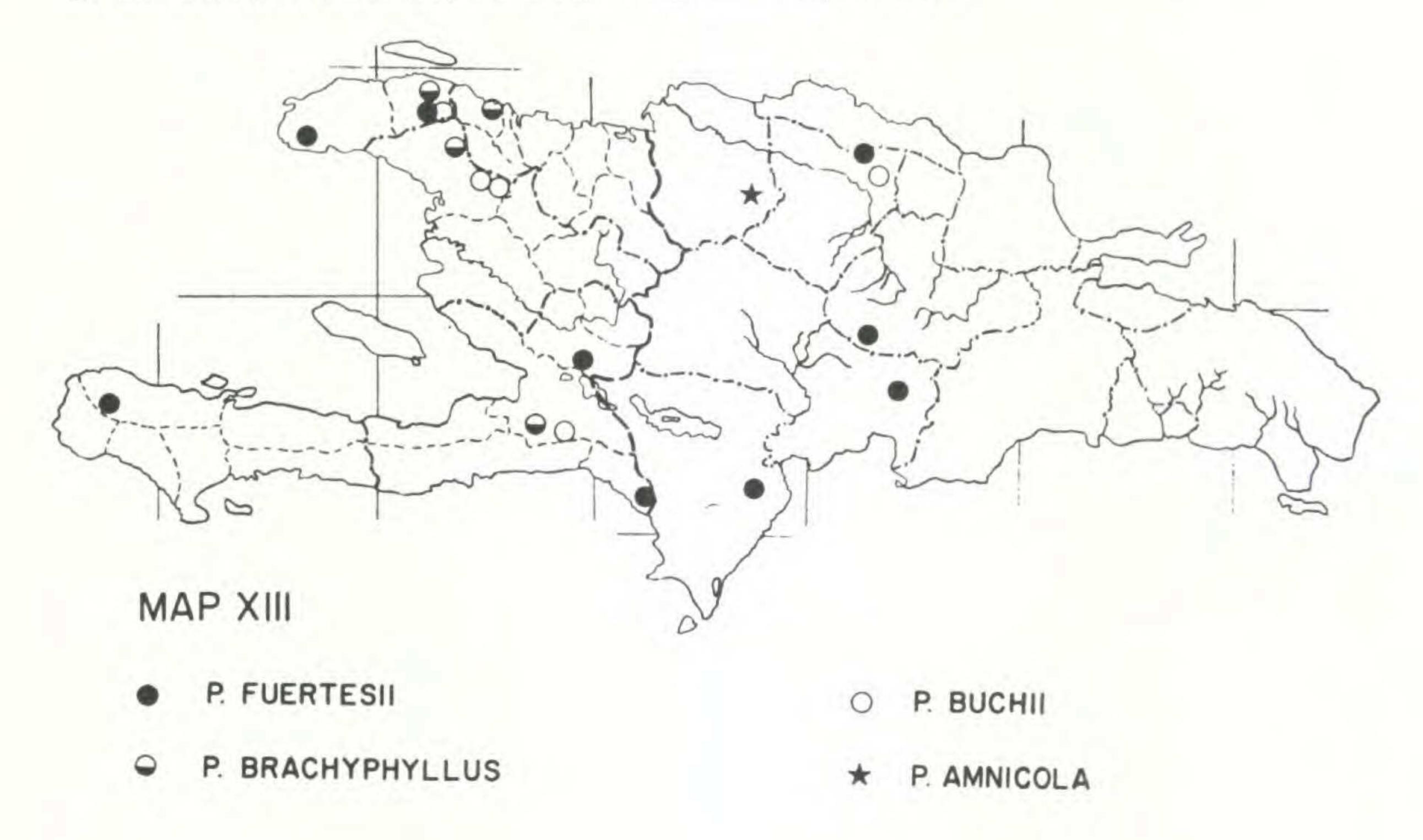
Phyllanthus micranthus ssp. fuertesii (Urb.) Webster, Contr. Gray Herb. 176: 55. 1955.

Sparsely branching annual or perennial herb or subshrub, c. 3-8 dm. high; main stems terete, smooth or with a few scattered raised striae, brown or grayish, 1-3 mm. thick, with internodes mostly 2-5 cm. long beneath, decreasing to 0.5-2 cm. long above. Cataphylls: stipules triangular-ovate, 1.2-1.8 mm. long, 0.6-0.9 mm. broad, acuminate, dentate, conspicuously auriculate, at first reddish and scarious becoming dark and rigid, or reddish-black and indurate from the first; blade linear-lanceolate, 0.9-1.1 mm. long. Deciduous branchlets (4-) 5-9 (-11) cm. long, 0.2-0.4 mm. thick, subterete or obtusely angled, smooth or the first internode roughened with raised striae, greenish or brownish, with mostly 20-40 (-45) leaves; first internode 3-6 mm. long, median internodes 2-4 mm. long. Leaves: stipules narrowly lanceolate, 0.6-1 mm. long, 0.2-0.25 mm. broad, acuminate, olivaceous becoming more or less reddish with age, scarious but not indurate. Leaf-blades membranous to chartaceous, smooth on both sides, narrowly oblong or oblong-lanceolate, (4-) 5-8 (-9) mm. long, 1.8-3 mm. broad, acute or obtuse-apiculate at the tip, obtuse to rounded at the base; above dark green, the midrib not prominent, the laterals obscure; beneath pale, the midrib raised, the laterals forming a rather obscure reticulum; margins slightly thickened, sometimes reddish-tinged, plane, smooth or minutely roughened.

Monoecious or subdioecious, or sometimes dioecious; floriferous branchlets typically with the (0-) 2–10 (-15) proximal nodes barren, the succeeding (5-) 7–15 (-25) nodes with racemiform cymules of 3 or 4 male flowers, the bracteoles yellowish-scarious; female flowers solitary in the distal axils.

Male flower: pedicel 0.5–1 mm. long. Calyx-lobes 6 (rarely 5), subequal, broadly elliptic to obovate or sometimes spathulate, 0.8–1.1 mm. long, c. 0.6–0.8 mm. broad, rounded or obtuse at the tip, entire, yellowish and scarious, the midrib unbranched. Disk-segments 6 (5), thin and flattened, roundish, c. 0.1–0.2 mm. across, entire or somewhat glandular and then crenulate in outline, but never massive and rugose. Stamens 3;

filaments united most of their length into a rather slender column (0.2–) 0.3–0.4 mm. high and c. 0.1–0.15 mm. thick; anthers shortly stipitate or subsessile atop the column, 0.15–0.2 mm. long, 0.2–0.25 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing obliquely; pollen grains finely reticulate, 20–25 μ long, 17–20 μ broad.





P. LEPTONEURUS

Maps XIII and XIV. Distribution of some species of subsect. Pentaphylli in Hispaniola.

Female flower: pedicel becoming 1.5–2.5 mm. long, terete and slender below, obtusely angled above, olivaceous. Calyx-lobes 6 (rarely 5), subequal, mostly obovate, becoming (0.9–) 1.1–1.5 mm. long, 0.7–1 mm. broad, rounded at the tip, entire, with broad yellowish or whitish scarious

margins, the midrib obscurely branched. Disk 6-(5-) lobed, the lobes thin, flat, triangular or lanceolate. Ovary often becoming rugulose after anthesis; styles ascending or spreading, 0.25-0.4 mm. long, bifid $\frac{1}{4}$ to $\frac{1}{2}$ their length, the arms spreading, the tips slender, recurved.

Capsule oblate, 2.2–2.4 mm. in diameter, shallowly sulcate, obscurely rugulose, yellowish-brown, not veiny. Columella 0.6–0.75 mm. long. Seeds trigonous, 1.1–1.2 (–1.3) mm. long, 0.8–0.9 mm. radially and tangentially, yellowish-brown, with c. 10–12 very delicate longitudinal striae, obscurely transversely barred.

Type: Dominican Republic, Barahona, Fuertes 561.

DISTRIBUTION: Hispaniola (MAP XIII).

HAITI. Nord-Ouest: Presquîle du Nord-Ouest, La Bombarde, Ekman H4511 (A, US); rocky slope, vicinity of Bombardopolis, alt. 610 m., E. C. & G. M. Leonard 13407, 13435, 13468 (US); vicinity of Bassin Bleu, Trail Moustique, E. C. & G. M. Leonard 14996, 15004 (US). Ouest: Massif des Matheux, Grand-Bois, road Thomazeau to Cornillon, limestone slopes, alt. 800–900 m., Ekman H5679 (S); Massif de la Selle, Port-au-Prince, Group Crête-à-Piquants, Morne Aux-Fourques, limestone, c. 1000 m., Ekman H5922 (S); Massif de la Selle, Morne Commissaires, Auses-à-Pitres Banane, at Río Pedernales, alt. 200 m., Ekman H6917 (S). Sud: Massif de la Hotte, western group, Jerémie, between La Source Chaude and Source-Cahouane, edge of river, alt. c. 150 m., Ekman H10223 (S, US).

DOMINICAN REPUBLIC. Santiago: Cordillera Septentrional, top of Loma Diego de Ocampo, c. 1250 m., Ekman H16324 (S). La Vega: Constanza, El Salto de Constanza, alt. 1200 m., Jiménez 2961 (US). Barahona: Barahona, in collibus apricis, alt. 275 m., Fuertes 561 (GH, Lectotype; C, F, G, S, Isotypes). Azua: Maniel de Ocoa [San José de Ocoa], alt. 300 m., Türckheim 3688 (BR).

This perplexing species is as variable as it is common and widespread in Hispaniola. Urban originally compared it with P. leptoneurus and P. micranthus (the latter confounded with P. procerus), both of which indeed resemble some forms of the present species. He distinguished P. micranthus by means of its 5-merous calyx and two sessile anthers; and the Fuertes collection further differs from P. micranthus in its broader leaves and monoecious inflorescence. However, examination of the several other collections of P. fuertesii show that it is, in fact, quite variable with regard to its supposedly diagnostic characters. The number of calyx-lobes is at least occasionally 5 in the following collections: Leonard & Leonard 14996, Ekman H6917, and Ekman H10223. The inflorescence is dioecious or transitional to that condition in Leonard & Leonard 14996, Ekman H6917, and Ekman H5922. The Ekman collection from the Massif de la Hotte has the habit of P. amnicola, but is monoecious and otherwise appears typical for P. fuertesii. The collection from Azua, Türckheim 3688, has exceptionally large male flowers with spathulate calyx-lobes up to 1.3 mm. long, and so closely resembles P. leptoneurus that it was originally annotated as that species; but it has the finely reticulate pollen grains

typical for *P. fuertesii*. These and other divergences from the mean make it difficult to characterize *P. fuertesii*, but at least in the typical form it may be separated from all the closely related species: from *P. micranthus* by the 3 stamens with obliquely dehiscing anthers, from *P. buchii* by its non-indurate stipules and subentire disk-segments; from *P. brachyphyllus* by its obliquely dehiscing anthers; and from *P. leptoneurus* by its pollen grains. Unfortunately the dioecious nature of all these related species makes identifications very difficult when only female individuals are at hand.

The occurrence of specimens which appear to be intermediate in one or more respects between this and the other species suggests that hybridization may well be a contributing factor to the systematic difficulties. Ekman H5679, which appears to be somewhat intermediate between P. fuertesii and P. buchii, has only 25% good pollen as one might expect if it represented a hybrid, but on the other hand it has produced good seed. However, Ekman H5922, which appears intermediate to about the same degree has nearly 100% good pollen. The admittedly crude evidence available from herbarium specimens is thus of no real assistance in determining if there is really any sterility effect consequent on hybridization, nor does it even demonstrate that crossing has actually occurred; but there does not appear to be any more reasonable hypothesis which accounts for the evident intergradation between species.

27. Phyllanthus brachyphyllus Urb. Repert. Sp. Nov. 13: 452-453. 1914.

Subshrub c. 0.5 m. high or less, the straight stiffly erect main stems clustered on a short caudex; stems terete, brownish or greyish, smooth, furrowed or roughened by discontinuous longitudinally raised striae, 1-1.5 mm. thick; internodes mostly 3-5 cm. long below, decreasing to 0.5-2 cm. long above. Cataphylls: stipules triangular-lanceolate, 1-1.5 mm. long, 0.5-1 mm. broad, acuminate, conspicuously auriculate at the base, subentire, becoming reddish-black and indurate; blade linear-lanceolate, 0.5-1 mm. long. Deciduous branchlets 1-4 (-6) cm. long, 0.2-0.4 mm. thick, subterete or obtusely angled, olivaceous, smooth or sometimes roughened in the first internode, with c. 15-35 (-45) leaves; first internode 1.5-3 mm. long, median internodes 0.5-1.8 mm. long. Leaves: stipules persistent or subpersistent, firm, triangular-lanceolate, (0.5-) 0.7-1 mm. long, 0.2-0.35 mm. broad. Petioles 0.2-0.4 mm. long. Leaf-blades firm, ovate or elliptic to narrowly oblong-lanceolate, (2-) 2.5-4 (-5) mm. long, (0.7-) 1-1.7 mm. broad, usually abruptly apiculate at the tip, obtuse to emarginate at the base; above olivaceous, the midrib not raised, the laterals obsolete; beneath slightly paler, the midrib plane or slightly raised, the laterals obsolete or 1-3 pairs evident but a reticulum of veinlets never visible; margins slightly thickened, plane, smooth, more or less reddish-tinged.

Dioecious. Male branchlets with the 2-7 (-14) proximal nodes barren, the succeeding nodes with racemiform cymules of 3-5 male flowers; bracte-

oles reddish-brown, scarious but not indurate, subpersistent. Female branchlets with c. 10–25 proximal nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel up to 0.5 mm. long. Calyx-lobes 6, subequal. broadly elliptic to obovate, 0.9–1.2 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6, irregularly roundish or rectangular, glandular-lobed but scarcely rugose, c. 0.1–0.15 mm. across. Stamens 3; filaments completely united into a rather stout column c. 0.4–0.5 mm. high and 0.15–0.2 mm. thick; anthers sessile atop the column, connectives compressed back-to-back, discrete or fused, c. 0.15–0.2 mm. long, 0.3 mm. broad; anther-sacs with confluent slits, dehiscing strictly horizontally; pollen grains finely reticulate, 20–25 μ long, 16–21 μ broad.

Female flower: pedicel 0.8–1.7 mm. long, olivaceous, rather stout, gradually dilated upwards, obtusely angled. Calyx-lobes 6, subequal, elliptic to obovate, 1–1.5 mm. long, 0.8–1.3 mm. broad, entire, olivaceous with broad yellowish-white scarious margins, the midrib unbranched. Disk 6-angled or obtusely 6-lobed, thin, plane. Styles more or less ascending, slender, c. 0.4–0.45 mm. long, parted ¼ to ⅓ their length, the branches only slightly divergent, the unthickened tips more or less recurved.

Capsule slightly over 2 mm. broad, yellowish-brown, obscurely rugulose at the top, not veiny. Seeds c. 1.2 mm. long, 1 mm. radially and tangentially, yellowish-brown, finely transversely barred (the longitudinal striae obscure or quite invisible).

Type: Haiti, Nash & Taylor 1718.

Distribution: mountainous areas, Haiti (Map XIII).

HAITI. Nord-Ouest: Massif du Nord, Port-de-Paix, Haut-Piton, open place on the eastern slope of the top, c. 1200 m. alt., 9 Aug. 1925, Ekman H4625 (S). Nord: Massif du Nord, Le Borgne, top of Morne Darras, alt. c. 1175 m., 3 Sept. 1925, Ekman H4772 (S, US). Artibonite: La Brande to Mt. Balance, sunny hillside, alt. 3300 ft., 15 Aug. 1905, Nash & Taylor 1718 (NY, Lectotype; US, ISOTYPE); Mt. Bellance [Belanse], Gros-Morne, in open stony slopes, alt. 1000 m., 26 Sept. 1925, Ekman H4915 (A, S). Ouest: Port-au-Prince, Morne Megi, Wegrand, alt. 1000 m., Aug. 1917, Buch 1422 (GH, JAM).

This species, which in many ways is intermediate between *P. fuertesii* and *P. buchii*, is here retained only with the proviso that its status must be considered dubious. At first it seemed likely that *P. brachyphyllus* might represent merely a hybrid between those two species; but there are several circumstances which make it difficult to assign it outright hybrid status. It was hoped that examination of the pollen might prove decisive in interpreting the situation, but unfortunately pollen was not available from most collections, and the results of the observations that were made proved to be inconclusive. *Ekman H4772*, for instance, had only about 20 percent good pollen, as one might expect if it represented a hybrid; but *Buch 1422* yielded nearly 100 percent good pollen. Furthermore, some collections of *P. buchii* (such as *Ekman H8410*) had a high percentage of defective

grains even though they appeared to represent the "pure" species. It still seems possible that study of the pollen can yield significant results, particularly if preserved material were available for cytological smears; but at present it must be admitted that no great help is forthcoming from this field.

Morphologically, *P. brachyphyllus* shows some features which cannot readily be dismissed as intermediate between *P. fuertesii* and *P. buchii*; the most important of these are the shorter branchlets, smaller leaves, and male flowers with a slightly longer staminal column and completely sessile horizontally dehiscing anthers. The known geographical distribution of *P. brachyphyllus* and its two possible parents is of little assistance, for the available specimens merely indicate a scattering of all three species over much of western Hispaniola. Thus although much suspicion attaches to the status of *P. brachyphyllus*, and its specific distinctiveness is very weak, it is here retained as a full species pending further investigation.

28. Phyllanthus buchii Urb. Symb. Ant. 3: 288-289. 1902. (PLATE XX, fig. D).

Subshrub c. 0.5-1.3 m. high, the sparsely branching main stems erect, smooth, terete, brownish, inconspicuously furrowed, mostly 1-2 mm. thick; internodes mostly 2-10 cm. long (becoming shorter at the tips). Cataphylls: stipules triangular-ovate, 1.2-1.9 (-2.3) long, 0.8-1.1 (-1.25) mm. broad, acute, conspicuously cordate-auriculate, subentire or crenately toothed, dark reddish becoming blackish and indurate; blade lanceolate, acuminate, 0.7-1.5 mm. long. Deciduous branchlets mostly 3.5-10 (-12) cm. long, 0.25-0.6 mm. thick, subterete, olivaceous, smooth, with (15-) 20-40 (-45) nodes; first internode 3-7 mm. long, median internodes 1.5-4 mm. long. Leaves: stipules persistent, lanceolate, 0.7-1.3 mm. long, 0.25-0.5 mm. broad, acuminate, entire, reddish when young, becoming reddish-black and indurate (sometimes with a very narrow whitish margin). Leaf-blades firm (subcoriaceous or coriaceous), smooth on both sides or scabridulous beneath (sometimes, scabridulous above), elliptic or oblong, mostly 3.5-8 mm. long, 1.5-3 mm. broad; above deep green or brownish, the midrib impressed, the laterals invisible; beneath olivaceous, paler, the midrib evident and continuing to the tip but scarcely raised, the laterals obsolete; margins thickened, often rim-like, smooth, plane.

Dioecious or subdioecious. Male branchlets with the (0-) 2-6 proximal axils barren, the racemiform cymules producing up to 5 or 6 male flowers and becoming almost 1 mm. long, the reddish-black entire somewhat indurate bracteoles persistent. Female branchlets with the proximal (3-) 6-16 axils barren, the flowers solitary at the succeeding nodes; occasional female flowers sometimes appearing on otherwise male branchlets.

Male flower: pedicel 0.5–1 mm. long. Calyx-lobes 6, subequal, elliptic to obovate, 0.8–1.1 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6, massive, conspicuously rugose-papillate, c. 0.15–0.25 mm. across. Stamens 3; filaments connate for most of their length into a stout column c. 0.3–

0.35 mm, high and 0.2–0.25 mm, broad; anthers short-stipitate to subsessile on the column, broadly ovate, blunt, 0.15–0.2 mm, long, 0.2–0.3 mm, broad; anther-sacs divergent, the slits apically confluent, dehiscing horizontally or obliquely; pollen grains finely reticulate, 21–30 μ long, 18–25 μ broad.

Female flower: pedicel becoming 1.5–2.5 mm. long, terete and reddish below, angled and olivaceous above. Calyx-lobes 6, subequal, elliptic or oblong to obovate, becoming 1.1–1.5 mm. long, 0.7–1.1 mm. broad, obtuse or rounded at the tip, entire, the yellowish- scarious margin conspicuous but not as broad as the olivaceous midstrip, the midrib pinnately branched but the veins all obscure. Disk 6-lobed, the lobes rather thick, obtuse, triangular. Styles ascending or spreading, somewhat thickened, 0.3–0.4 mm. long, parted ½ to ½ their length, the arms spreading, the slender unthickened tips recurved.

Capsule oblate, c. 2.5 mm. in diameter, shallowly sulcate, nearly smooth, yellowish-olivaceous, not veiny. Seeds trigonous, 1.3–1.4 mm. long, 0.9–1 mm. radially and tangentially, yellowish-brown, with c. 12 very tenuous longitudinal striae, transversely barred with slightly hygroscopic epidermal cells.

Type: Haiti, Buch 251.

DISTRIBUTION: mountainous areas, Hispaniola (MAP XIII).

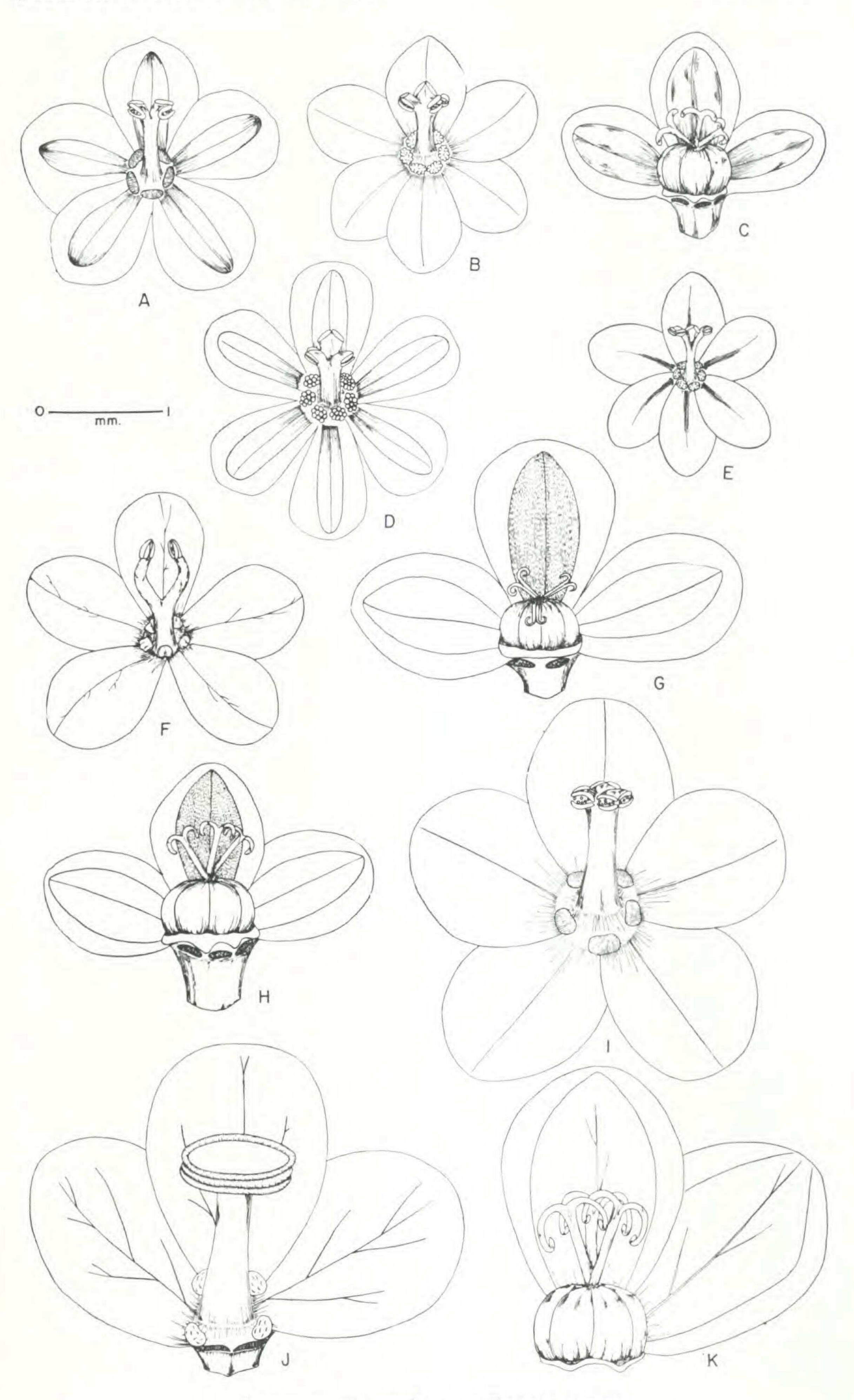
HAITI. Nord: grassy slope, M. la Cidre, alt. 350 m., vicinity of St. Michel de l'Atalaye, 23 Nov. 1925, Leonard 7402 (US). Artibonite: Ennery, Buch 251 (NY, Lectotype; GH, Isotype); hills near Ennery, low forest with some pines on soft limestone, alt. c. 600 m., 14 Nov. 1924, Ekman H2466 (S, US); hills north of Ennery, pineland, alt. 550 m., 12 June 1927, Ekman H8410 (S, US); vicinity of Ennery, Puilboreau road, alt. 325–900 m., 21 Jan. 1926, Leonard 9061 (US), 9064 (GH, US). Ouest: Massif de la Selle, Ganthier, ridge of M. Vincent, above Source-Courty, alt. c. 1700 m., 2 Mar. 1927, Ekman H7757 (S).

DOMINICAN REPUBLIC. Santiago: Las Lagunas, hills at Arroyo Harenquillo, alt. c. 400 m., 20 Oct. 1930, Ekman H16077 (S). Barahona: Aceitillar, Sierra de Bahoruco, 13 Nov. 1955, coll. Prof. Marcano, Jiménez 3121 (US).

In its typical form, *P. buchii* is readily recognizable by virtue of its coriaceous leaves, darkened indurate branchlet stipules and male flowers with obliquely dehiscing anthers and rugose-papillate disk-segments. However, specimens intermediate between *P. buchii* and *P. fuertesii* occur (as

PLATE XX. FLOWERS OF SECT. Phyllanthus, Subsect. Pentaphylli.

Fig. A. Phyllanthus micranthus A. Rich. (Linden 2074 [A]). Figs. B-C. Phyllanthus fuertesii Urb. (Fuertes 561 [GH]). Fig. D. Phyllanthus buchii Urb. (Buch 251 [GH]). Fig. E. Phyllanthus amnicola Webster (Ekman H12936 [S]). Figs. F-G. Phyllanthus maestrensis Urb. (male, Morton & Acuna 3825 [US]; female, Ekman 7247 [S]). Figs. H-I. Phyllanthus leptoneurus Urb. (Ekman H11505 [S]). Figs. J-K. Phyllanthus dimorphus Br. & Wils. (Webster 4770 [GH]).



Webster, West Indian Phyllanthus

discussed under the latter species), and hybridization very probably plays a part in contributing to the difficulty in distinguishing P. buchii from its neighbors. Furthermore, considerable geographical variation is evident, which may be due largely to the fact that the species grows only in the mountains and is consequently broken up into many small populations on individual peaks. The specimen from Arroyo Harenquillo ($Ekman\ H16077$), which has a somewhat different aspect from the Haitian collections, has associated in a packet on the sheet a single seed 1.5 mm. long which is verruculose, with evenly spaced round points, rather than being striate, as in other collections of the species. If this seed really belongs with the plant, then $Ekman\ H16077$ probably represents a distinct undescribed species; but since the collection shows no other really distinctive features, it is retained for the present within P. buchii.

29. Phyllanthus amnicola Webster, Contr. Gray Herb. 176: 54. 1955. (PLATE XX, fig. E).

Decumbent annual or short-lived perennial herb, the sparsely branching main stems c. 1.5-3 dm. long, 0.7-1.3 mm. thick, subterete, brownish, smooth on older portions, more or less roughened with minute pale ridges above; stems more or less rooting at the lower nodes; internodes mostly 0.5-2.5 cm. long. Cataphylls: stipules triangular, (1.2-) 1.5-2 mm. long, 0.7-0.8 mm. broad, short-acuminate, conspicuously auriculate at the base, entire or sparsely toothed, becoming blackish and indurate; blade linearlanceolate, c. 0.5-1 mm. long. Deciduous branchlets (2-) 4-8 (-12) cm. long, 0.25-0.3 mm. thick, subterete, olivaceous, densely short-hispidulous, with mostly 20-50 (-70) leaves; first internode (1.5-) 2-4 (-5) mm. long, median internodes (1-) 1.5-2.5 (-3) mm. long. Leaves: stipules subpersistent, lanceolate, 0.5-0.8 mm. long, c. 0.3 mm. broad, acuminate, reddisholivaceous becoming dark reddish-brown, scarious. Petioles 0.3-0.5 mm. long. Leaf-blades firmly chartaceous, oblong, usually somewhat falcate, c. 3-6 mm. long and 1.5-2.3 mm. broad, obtuse or rounded at the tip (mostly with no trace of an apiculum even when young), obtuse at the base; above plumbeous-olivaceous, minutely foveolate, plane or depressed along the midrib; beneath greyish-pulverulent, conspicuously hispidulous, the midrib prominent, the 2-4 pairs of laterals slightly raised, straight, not anastomosing; margins conspicuously thickened and revolute, smooth.

Dioecious. Male branchlets mostly with the proximal 1–4 nodes barren, the succeeding nodes with racemiform cymules of 3 or 4 male flowers; bracteoles reddish-brown, scarious. Female branchlets [only a few observed] with the proximal 7–10 nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel c. 0.8–1.3 mm. long. Calyx-lobes 6 (rarely 7), subequal, obovate, c. 0.7–0.9 mm. long, 0.5–0.75 mm. broad, rounded at the tip, entire, yellowish and scarious, the midrib unbranched. Disk-segments 6, concave, thin, crenulate or entire, roundish, not glandular, c. 0.15–0.2 mm. across. Stamens 3; filaments c. 0.4–0.5 mm. long, united in

the lower half into a column; anthers nearly reniform in outline, very obtuse, c. 0.15 mm. long, 0.2–0.3 mm. broad; anther-sacs widely divergent, the slits confluent, dehiscing horizontally or somewhat obliquely; pollen

grains finely reticulate, c. $18-22\mu$ long, 15-18 μ broad.

Female flower [not seen at anthesis]: pedicel 1–1.2 mm. long, olivaceous, smooth or slightly roughened, subterete, gradually dilated from the base. Calyx-lobes 6, subequal, obovate, c. 1–1.2 mm. long, 0.6–0.8 mm. broad, rounded at the tip, entire, olivaceous with broad conspicuous whitish-scarious margins. Disk [as seen in fruit] parted into 6 linear-lanceolate subacute segments. Ovary and styles not seen.

Capsule not seen entire; valves c. 1.7–1.8 mm. long, olivaceous, smooth, not veiny; seeds c. 1.1 mm. long, 0.7–0.85 mm. radially and tangentially,

yellowish-brown, finely striate longitudinally and transversely.

Type: Dominican Republic, Prov. Monte Cristi, Monción, at the junction of the Río Cenobí and the Río Cenobicito, edge of stream, alt. 700 m., 20 June 1929, Ekman H12936 (S, HOLOTYPE; US, ISOTYPE).

DISTRIBUTION: known only from the type collection (MAP XIII).

This very distinctive species, named in allusion to its riparian habitat, may at once be distinguished from its relatives by its conspicuously hispidulous branchlets and lower leaf-surfaces, as well as by its only partially united stamens and dissected female disk. It is perhaps most closely related to *P. fuertesii*, some forms of which (e.g., *Ekman H10223*) also grow in stream-beds and have a similar habit; but these lack the characteristic vegetative and floral characters of *Ekman H12936* from Monción. Consequently, it seems evident that *P. amnicola* is a distinct species rather than merely an ecological variant of *P. fuertesii*.

30. Phyllanthus maestrensis Urb. Symb. Ant. 9: 193. 1924. (PLATE XX, figs. F-G).

Suffruticose glabrous perennial 0.5-1.5 m. high, the main stem erect, stiff or wand-like, simple or sparsely branched above, greyish and sometimes sulcate above, smooth and brownish below; internodes mostly 2-6 cm. long. Cataphylls: stipules triangular, (1-) 1.2-1.8 (-2) mm. long, 0.5-1 mm. broad, acute to acuminate, conspicuously auriculate at the base, entire or more often denticulate towards the base (sometimes with conspicuous lateral teeth near the apex), reddish-brown becoming indurate and blackened; blade lanceolate, 0.8-1.5 mm. long, 0.2-0.3 mm. broad. Deciduous branchlets mostly 7-15 cm. long, 0.25-0.4 (-0.5) mm. thick, terete or obscurely angled, smooth, brownish or greenish, with mostly 30-50 leaves; first internode 3-12 (-16) mm. long, median internodes 2-4 (-5.5) mm. long. Leaves: stipules lanceolate, 0.9-1.5 mm. long, 0.25-0.4 mm. broad, acuminate or attenuate-acuminate, basally dilated, reddish becoming blackened in the distal half, scarious, entire. Petioles 0.3-0.7 mm. long. Leaf-blades membranous to chartaceous, oblong or ellipticoblong, 6-13.5 mm. long, 2-5 mm. broad, obtuse or rounded to subtruncate and usually apiculate at the tip, tapering more or less evenly at the base; above olivaceous, the midrib and laterals usually slightly raised (at least proximally); beneath pale yellowish- or greyish-green, the midrib raised, the laterals (c. 5–8 on a side) plane but dark and conspicuous, the delicate tertiaries visible or obsolete; margin scarcely thickened, plane, smooth.

Monoecious or exceptionally subdioecious, the male and female flowers usually on the same branchlets; (0–) 2–15 (–20) proximal nodes barren, succeding (5–) 10–20 (–25) nodes with racemiform cymules of 3–7 male flowers, distal nodes with solitary female flowers.

Male flower: pedicel 0.5–0.7 mm. long. Calyx-lobes 5, broadly obovate to spathulate, (0.8–) 1–1.2 mm. long, 0.6–0.9 (–1.1) mm. broad, broadly obtuse or rounded at the tip, entire, yellowish-scarious with an olivaceous median area, the midrib unbranched or with 1 or 2 ascending lateral veins. Disk-segments 5, more or less elliptical, 0.15–0.25 mm. across, smooth, subentire. Stamens 2; filaments 0.5–0.75 mm. long, fused in the lower $\frac{1}{3}$ to $\frac{2}{3}$ their length into a stout column c. 0.25–0.3 mm. thick; anthers introrse, erect, 0.2–0.3 mm. long, 0.3–0.35 mm. broad; anther-sacs somewhat divergent, contiguous apically and thus usually with an apically confluent slit, dehiscing vertically and laterally; pollen grains finely reticulate, 23–28 μ long, 18–23 μ broad.

Female flower: pedicel 1.5–2.5 mm. long. Calyx-lobes 5 (rarely 6), elliptic-obovate or spathulate, (1.1–) 1.3–2 (–2.3) mm. long, 0.9–1.1 mm. broad, obtuse or rounded at the tip, olivaceous with broad conspicuous yellowish scarious margins, the unbranched midrib slightly carinate dorsally. Disk rather massive, more or less minutely foveolate, obtusely 5-lobed or cut into 5 distinct segments. Styles free, ascending or at length spreading, 0.35–0.4 mm. long, bifid 1/4 to 2/5 their length, the branches spreading and recurving with tapering blunt or minutely uncinate tips.

Capsules not seen entire; valves yellowish-brown, smooth, not veiny. Seeds acutely trigonous, 1.2–1.4 mm. long, 0.9–1.1 mm. radially, 0.85–1.15 mm. tangentially, pale yellowish-brown, with c. 9–12 delicate longitudinal striae; epidermal cells not hygroscopic.

Collected in flower and fruit April throughout September.

Type: Cuba, Sierra Maestra, Ekman 7247.

DISTRIBUTION: endemic to Cuba (MAP XII).

CUBA. Pinar del Río: Pinar del Río, among tall grasses in thickets surrounded by pine woods, Wright 3684 ex p. (P, S; mixed with P. procerus); Arroyo del Sumidero, rocks near water, Shafer & León 13584 (NY); Vinales, Sitio del Infierno, in pineland hills, Ekman 16713 (S); San Diego de los Banos, Britton et al. 6799 (NY), León & Hioram 4443 (NY), Palmer & Riley 650 (NY, US). Oriente: Sierra Maestra, La Bayamesa, banks of the Río Oro, alt. 400 m., Ekman 7247 (S, HOLOTYPE), Webster 4119 (MICH); banks of Guama River, near Santiago de Cuba, Clemente 3409 (MICH).

A specimen from the Sierra Maestra, Pinar de Papayo (Ekman 9267

[S]), has male flowers with introrse anthers and is therefore referable to P. maestrensis, but it has not been accounted for in the description since it is aberrant in several respects: branchlets only 3.5-7.5 cm. long, leaves 4.5-6 mm. long, plants dioecious, filaments completely united and anthers sessile. It appears to be intermediate between P. maestrensis and P. micranthus and perhaps represents a hybrid between these two species.

Phyllanthus maestrensis is immediately distinguishable from its West Indian congeners by its introrse anthers, which in fact appear to be unique in the genus. Vegetatively, it perhaps most closely resembles P. dimorphus and P. leptoneurus; but in Cuba, it is most apt to be confused with either P. procerus or P. micranthus. Probably its closest relationship is with the latter species, but it apparently may hybridize with either. The apparent cross with P. micranthus has been noted above, and a specimen from Pinar del Río (Ekman 17875 [S]) intermediate between P. maestrensis and P. procerus has already been noted under the latter.

31. Phyllanthus leptoneurus Urb. Symb. Ant. 7: 246–247. 1912. (PLATE XX, figs. H-I; PLATE XXII, fig. A).

Phyllanthus trigonus Urb. & Ekm. Ark. Bot. 20A(15): 46-47. 1926.

Subshrub up to c. 7.5 dm. high, the subsimple main stem brownish, sometimes shiny, usually terete or obtusely angled (rarely with sharp decurrent ridges from the nodes), nearly smooth or with minute greyish longitudinal ridges, c. 1.5-2 mm. thick, internodes mostly 0.5-2 cm. long, or up to 5 cm. below. Cataphylls: stipules triangular-ovate or triangular-lanceolate, (1.2-) 1.5-2 mm. long, (0.6-) 0.8-1.2 mm. broad, acuminate, conspicuously auriculate at the base, entire or sparingly toothed, becoming reddishblack and indurate; blade linear-lanceolate, 0.9-1.5 mm. long. Deciduous branchlets mostly 5-15 (-18) cm. long (occasional ones shorter), (0.2-) 0.3-0.5 mm. thick, olivaceous or brownish, subterete or obtusely angled, proximally roughened with minute points or ridges (particularly on the first internode) or less commonly the entire length, with mostly 20-50 (-85) leaves; first internode (2.5-) 4-8 (-10) mm. long, median internodes 1.5-4.5 mm. long. Leaves: stipules persistent or subpersistent, ovate-lanceolate to linear-lanceolate, (0.5-) 0.7-1.2 mm. long, acuminate, olivaceous becoming more or less dark reddish and scarious (particularly at the tip). Petioles 0.3-0.7 mm. long. Leaf-blades membranous to chartaceous, elliptic to oblong, (4-) 5-11 (-13) mm. long, 2-4 (-5) mm. broad, mostly obtuse to truncate and apiculate at the tip, cuneate to obtuse at the base; above dark olivaceous, the midrib pale and conspicuous but not much raised, the laterals not visible; beneath distinctly paler, the midrib prominent and slightly raised, the laterals (c. 5-7 on a side) conspicuous and enclosing a fine reticulum, or sometimes obscure; margins scarcely or not at all thickened, plane, smooth or slightly roughened.

Dioecious. Male branchlets often longer than the female, the proximal (1-) 2-5 (-7) nodes barren, the succeeding nodes with racemiform cymules of 3-10 flowers, bracteoles yellowish-white or reddish-tinged,

scarious (not indurate), subpersistent. Female branchlets with the proximal 3-16 nodes barren, the succeeding nodes with solitary female flowers.

Male flower: pedicel (0.5–) 0.9–1.2 mm. long. Calyx-lobes 6 (less commonly 5), obovate to spathulate, c. 1.2–1.5 (–1.7) mm. long, 0.7–1.5 mm. broad, rounded at the tip, entire, yellowish-scarious, the midrib unbranched. Disk-segments 6 (5), roundish, rather thin, flat or slightly concave, entire, not glandular, mostly 0.2–0.3 mm. across. Stamens 3; filaments completely united into a column (0.5–) 0.7–0.9 mm. long and c. 0.2–0.3 mm. thick; anthers sessile, more or less connate back-to-back by the connectives, triangular to ovate, subacute or obtuse, 0.2–0.3 mm. long, 0.35–0.5 mm. broad; anther-sacs dorsiventrally compressed, divergent, the slits confluent, dehiscing horizontally; pollen grains coarsely reticulate (the brochi 1.5–3 μ across), nearly spheroidal, 24–30 μ long, 21–27 μ broad.

Female flower: pedicel becoming (1.5–) 1.8–2.5 mm. long, olivaceous, smooth or obscurely roughened, gradually dilated from the base, angled above or throughout. Calyx-lobes 6 (occasionally 5), subequal, obovate or sometimes spathulate, c. (1.2–) 1.3–1.8 mm. long, 0.9–1.4 mm. broad, rounded at the tip, entire, olivaceous with conspicuous pale scarious margins, midrib unbranched or with a few obscure steeply ascending lateral veins. Disk shallowly cupuliform, subentire or obscurely and obtusely 6-lobed. Styles erect or ascending, c. (0.3–) 0.5 mm. long, slender, parted ½ to ⅓ their length, the arms divergent, the slender tips recurved.

Capsule oblate, trigonous, c. 2.5 mm. in diameter, smooth, yellowish-brown, not veiny. Seeds plumply trigonous, c. 1.2 mm. long and 0.8 mm. radially and tangentially, pale yellowish-brown, with 8-10 plane longi-

tudinally darker bands and many fine transverse striae.

Type: Dominican Republic, Türckheim 3187.

Distribution: mountainous areas, Hispaniola (Map XIV).

HAITI. Nord: near Port Margot, Morne Maleuvre, shrubby grassy slopes, alt. 800–1000 m., 8 Dec. 1924, Ekman H2792 (S, Holotype of P. trigonus). Artibonite: Massif des Matheux, Grand-Bois, Morne Moitié-Duporté, on the high ridge, "Laubwald", limestone, alt. 1850–1875 m., 16 Mar. 1926, Ekman H5731 (A, S).

DOMINICAN REPUBLIC. Duarte [formerly in Pacificador]: Loma Quita Espuela, vicinity of San Francisco de Macorís, alt. 400–1000 m., 5–17 Apr. 1922, Abbott 2132 (US), 2138 (NY, US); top of Loma Quita Espuela, alt. 930 m., 25 Apr. 1929, Ekman H12288 (S). La Vega: Constanza, Valle Nuevo, Kiefernwald unterhalb, alt. 1700 m., Apr. 1910, Türckheim 3187 (BR, Lectotype). Trujillo Valdez [formerly in Azua]: Sierra de Ocoa, San Jose de Ocoa, Bejucal, Loma de los Palos Mojados, alt. c. 1650 m., in pinelands, 13 Mar. 1929, Ekman H11919 (S, US). Santo Domingo: top of Loma La Campana (west of La Cumbre), alt. c. 1100 m., 11 Feb. 1929, Ekman H11505 (S).

This robust species is usually recognizable as distinct from its Hispaniolan congeners by virtue of its longer branchlets with more leaves which are usually truncate at the tip, larger male flowers, with completely united filaments, and banded rather than striate seeds. Actually its coarsely reticulate pollen grains are its most characteristic feature, and examination of these will always permit discrimination of the present species from superficially similar forms of *P. fuertesii*. It is possible that hybridization may occasionally occur between these two species, as a rather intermediate specimen from San Jose de Ocoa (*Türckheim 3688*; listed under *P. fuertesii*) suggests. There can be no doubt, however, that the only near relative of *P. leptoneurus* is the following species, *P. dimorphus*, which also has coarsely reticulate pollen grains and is very similar in its vegetative parts and flowers as well.

32. Phyllanthus dimorphus Br. & Wils. Mem. Torr. Bot. Club 16: 75. 1920. (PLATE XX, figs. J-K).

Subshrub c. 0.5-1.5 m. high, the erect main stem subsimple, 1.5-2.5 mm. thick, terete or nearly so, brownish and smooth on older basal portions, plumbeous with many fine pale longitudinal ridges above; internodes c. 3-7 cm. long below, 0.5-2 cm. above. Cataphylls: stipules ovate-lanceolate, 1.5-2.5 (-3) mm. long, 1-1.5 (-2) mm. broad, acuminate, conspicuously auriculate at the base, subentire, blackish and indurate; blade lanceolate, more or less reflexed, c. 0.8-1.5 (-2) mm. long, 0.3 mm. broad. Deciduous branchlets (4-) 5-15 (-22) cm. long, 0.4-0.7 mm. thick, subterete, plumbeous or brownish, more or less roughened with minute ridges on the main stem (especially so on the first internode), with 25-75 (-95) leaves; first internode 1.5-4.5 mm. long, median internodes (1-) 1.5-3.5 mm. long. Leaves: stipules persistent, triangular-lanceolate, 0.7-1.5 (-2.2) mm. long, 0.3-0.7 mm. broad, acuminate, dark reddishbrown to black, more or less indurate. Petioles 0.4-0.5 mm. long. Leafblades subcoriaceous, linear-oblong, 6-11 mm. long, 1.5-4 (-5) mm. broad, obtuse to rounded and apiculate at the tip, obtuse at the base; above deep olivaceous, smooth, the midrib plane, the laterals invisible, beneath brownish with minute white flecks or greyish, the midrib prominently raised, the laterals (c. 3-6 on a side) rather obscure or obsolete; margins thickened, plane, smooth or minutely roughened, more or less reddishtinged.

Dioecious or rarely monoecious (but then the branchlets unisexual). Lower branchlets of male plant with c. 10–40 barren proximal nodes, upper with c. 5–8 such barren nodes, the succeeding nodes with racemiform cymules of 3 or 4 flowers; bracteoles reddish-brown, scarious, subpersistent. Female branchlets with c. 15–25 barren proximal nodes, the succeeding nodes with solitary female flowers.

Male flower: pedicel c. 0.7–1.8 mm. long. Calyx-lobes 5, subequal, elliptic-obovate, c. (1.4–) 1.7–2 (–2.3) mm. long, 0.9–1.7 (–2) mm. broad, broadly rounded at the tip, entire, yellowish-scarious, the midrib unbranched or nearly so. Disk-segments 5, trigonous, fleshy and massive, subentire, not evidently glandular, c. 0.25–0.4 mm. across. Stamens 3,

completely fused into a synandrium as in sect. *Cyclanthera*, the column 1.1–1.3 mm. high, c. 0.35 mm. thick at the dilated base, tapering above; common connective of the synandrium plane or with the slight central umbo, peltate on the column, c. 0.5 mm. across (the entire synanther c. 0.7–1 mm. across); anthers horizontal, confluent into a circumscissile rim encircling the connective; pollen grains coarsely reticulate, 20–25 μ long, 19–24 μ broad.

Female flower: pedicel becoming (2.2–) 2.5–2.8 (–3.1) mm. long, subterete, smooth, olivaceous or reddish-brown. Calyx-lobes 5, elliptic to obovate, 1.6–2.5 mm. long, 1–1.6 mm. broad, rounded at the tip, entire, with fairly broad yellowish-scarious margins, the midrib apparently unbranched (the lateral veins completely obscure), not dorsally carinate. Disk saucer-shaped, obscurely 5-lobed or 5-angled, entire. Styles erect, 1.1–1.7 mm. long (much longer than the ovary), parted ¼ to ⅓ their length, the branches divergent, the slender recurved tips 0.4–0.7 mm. long.

Capsule oblate, 2.8–3 mm. in diameter, shallowly sulcate, olivaceous, obscurely rugulose, not veiny; seeds plumply trigonous, 1.2–1.3 mm. long, 1–1.1 mm. radially and tangentially, light yellowish-brown, lucent, with c. 10–12 fine longitudinal scarcely raised striae, finely transversely striate.

Type: Cuba, Trinidad Mountains, Britton & Wilson 5350.

DISTRIBUTION: endemic to the Trinidad Mountains, Cuba (MAP XII).

CUBA. Las VILLAS: Trinidad Mountains, El Porvenir to Aguacate, grassy hill, alt. 700–900 m., 10 Mar. 1910, Britton & Wilson 5350 (NY, HOLOTYPE; F, US, ISOTYPES); Buenos Aires, alt. c. 2500 ft., 6 Dec. 1928, Jack 6849 (A, F, US; flowers abnormal), 6 Mar. 1929, 7003 (A); same locality, 12 Mar. 1930, Hunnewell 11571 (GH); Loma del Campo, Buenos Aires, grassy shrubby area, 19 July 1953, Webster 4770 (GH).

The floral morphology of this species was completely misinterpreted by Britton & Wilson, who described the flowers as having the styles slender and forked in some plants and united in a column with a peltate stigma in others. Since in the latter instance they were actually describing the characteristic androecium of the species, their epithet *dimorphus* is unfortunately inappropriate and erroneous.

The synandrium of this species superficially closely resembles that of species in sect. Cyclanthera, and Alain (Fl. Cuba 3: 56. 1953) has in fact combined P. dimorphus with P. cyclanthera [i.e., P. lindenianus]. However, the pollen grains and stipules clearly demonstrate that the plant of the Trinidad Mountains belongs to subsect. Pentaphylli of sect. Phyllanthus. Furthermore, the coarsely reticulate ornamentation of the pollen, as well as vegetative features, show that P. dimorphus is much more closely related to P. leptoneurus of Hispaniola than it is to any of the Cuban species.

33. Phyllanthus junceus Muell. Arg. in DC. Prodr. 15(2): 411-412. (PLATE XXI, figs. A-B).

Phyllanthus pruinosus var. ? subnudus Wright ex Griseb. Cat. Pl. Cub. 16. 1866.

Phyllanthus squamatus Wright, Anal. Acad. Ci. Habana 7: 109–110. 1870. Diasperus junceus (Muell. Arg.) O. Ktze. Rev. Gen. 2: 599. 1891.

Perennial herb, main axis a slender more or less gnarled woody caudex bearing at ground level several clustered wand-like branches mostly 1-3.5 dm. high, 0.5-1 (1-1.3) mm. thick, stramineous to pale reddish-brown, smooth, terete, sulcate, with (3-) 5-7 (-10) nodes, the internodes mostly 2-6 (-8) cm. long. Cataphylls: stipules ovate, 1.2-1.8 mm. long, 0.6-1.1 mm. broad, acute or acuminate at the tip, basal auricle very large (and often overlapping so that stipule appears peltate) and denticulate, brownish-black and indurate; blade lanceolate, 0.5-0.8 mm. long. Deciduous branchlets mostly 2-7 (-8) cm. long, 0.2-0.4 mm. thick, light brownish, somewhat pruinose, smooth, terete, with c. (6-) 10-20 (-30) leaves; first internode (6-) 10-18 (-25) mm. long, median internodes 2-4 (-6) mm. long. Leaves: stipules mostly ovate-lanceolate, 0.6-0.8 (-1.1) mm. long, 0.25-0.4 mm. broad, acute or acuminate at the tip, entire, dark brown to blackish and more or less indurate. Petioles 0.3-0.6 (-0.8) mm. long. Leaf-blades chartaceous to subcoriaceous, elliptic to obovate, mostly 5-8 (-10) mm. long and 2-5 mm. broad, obtuse or rounded at both ends; above olivaceous, minutely but usually distinctly areolate-foveolate, the midrib inconspicuous, the laterals obscure; beneath minutely pulverulentscabridulous (glabrate with age), the midrib raised, the laterals obsolete; margins thickened, smooth, sometimes more or less revolute.

Dioecious or subioecious, the branchlets never bisexual; proximal 1–3 axils barren, or all nodes floriferous; male flowers c. 7–10 in racemiform cymules which become 1–1.5 mm. long, the bracteoles subindurate; female

flowers solitary.

Male flower: pedicel c. 1.2–2.2 mm. long. Calyx-lobes 5, elliptic to spathulate, 1–1.5 (–1.7) mm. long, 0.6–0.9 (–1) mm. broad, obtuse or rounded at the tip, entire, yellowish, the herbaceous median area narrower than the broad scarious margins, the midrib unbranched. Disk-segments 5, squarish or broadly obcuneate, c. 0.2–0.3 mm. across, thin, subentire, usually standing erect. Stamens 2 (rarely 3, or with the rudiment of a third); filaments united into a colmun (0.4–) 0.5–0.6 (–0.75) mm. high, gradually tapering from the strongly dilated base to the apex; anthers sessile or subsessile atop the column, discrete or sometimes slightly connate by the connectives, 0.2–0.3 mm. long, 0.25–0.4 mm. broad; anthersacs divergent, confluent at the apex, dehiscing more or less horizontally; pollen grains finely reticulate, 23–27 μ long, 18–22 μ broad.

Female flower: pedicel becoming (2.2-) 2.5-3 (-4) mm. long, more or less terete below, angled and thickened above. Calyx-lobes 5 (rarely 6), elliptic to spathulate, becoming 1.5-1.8 (-2) mm. long, (0.75-) 0.9-1.5 mm. broad, rounded or obtuse at the tip, with broad scarious margins, the midrib raised dorsally and ventrally, the lateral veinlets usually quite inconspicuous. Disk 5-lobed or nearly divided into 5 (6) suborbicular segments, somewhat fleshy, entire, sometimes pitted. Styles free, ascend-

ing, 0.3-0.45 mm. long, parted only ¼ their length, the more or less flattened and dilated style-branches recurved.

Capsule [rarely seen entire] c. 3.5 mm. in diameter, smooth, light brownish, not veiny. Seeds (1.35–) 1.5–1.7 (–1.8) mm. long, c. 1–1.2 mm. radially and tangentially, golden- or chestnut-brown, transversely barred with overlapping rows of more or less hygroscopic cells which spread as brownish setae when wetted, the longitudinal striae very inconspicuous or invisible.

Collected in flower and fruit November to July; perhaps flowering throughout the year.

Type: Cuba, Pinar del Río, Wright 1937.

DISTRIBUTION: endemic to western Cuba and the Isle of Pines (Map XV).

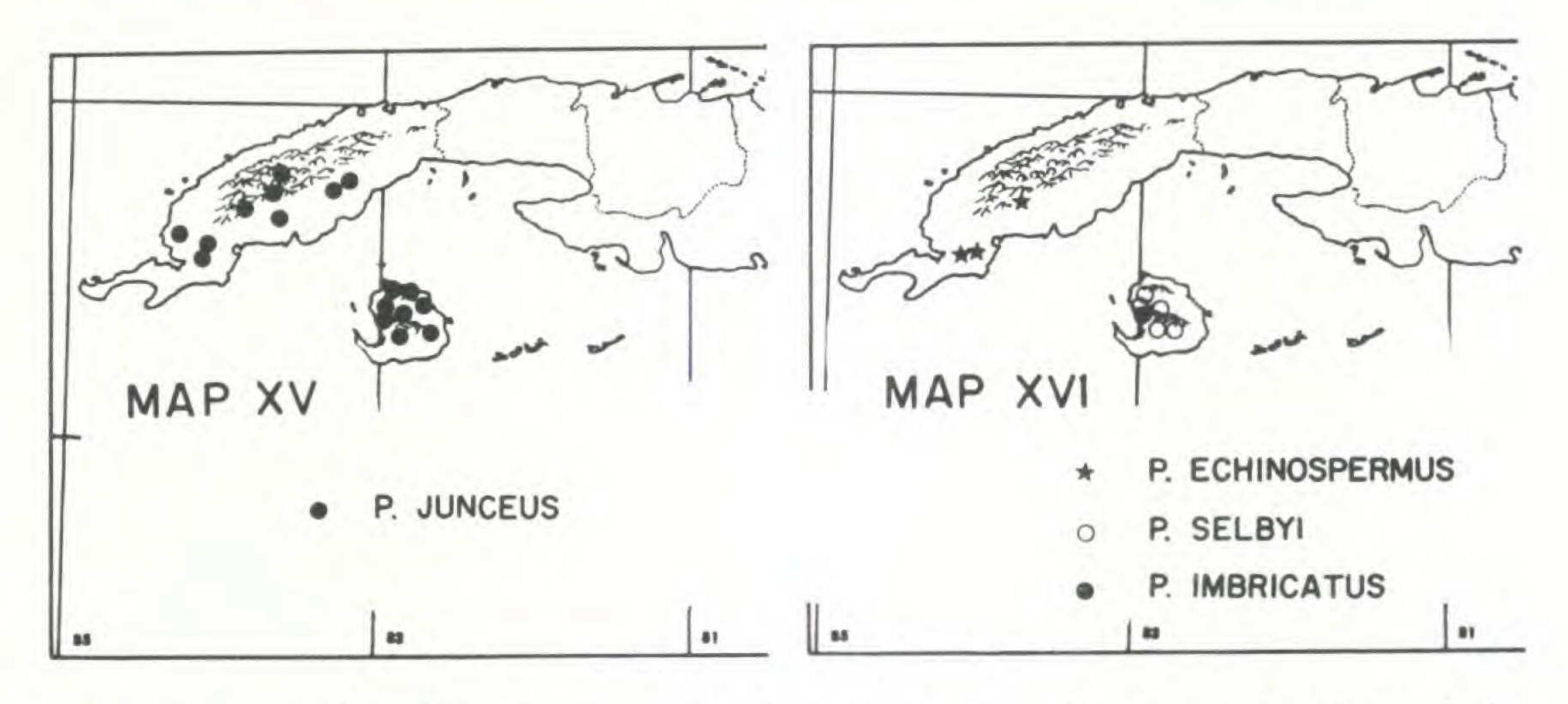
CUBA. Pinar del Río: Arroyo Mantua, Damují, in savannas near salt water, Ekman 11067 (S); palm-barrens west of Guane, Shafer 10628 (NY); Laguna Jovero to Mendoza, in sand, Shafer 10875 (NY); cut-over pineland between Pinar del Río City and Sumidero, Webster 4671 (GH); pinelands near Pinar del Río, Wright 3685 (GH, NY; type collection of P. squamatus); pinelands near San Luis, south of Pinar del Río, León et al. 19589 (MICH); savanna 10.5 km. south of Pinar del Río, Proctor 16329 (JAM); white sands near lagoons, between Pinar del Río and La Coloma, Webster 4675 (GH); between Vinales and Pinar del Río, serpentine bank, Webster 4669 (GH); Vinales, Sitio del Infierno, in pineland hills, Ekman 16722 (S); Herradura, pinelands, Baker 3503, Britton et al. 6448, Earle 642 (NY); between Los Palacios and Herradura, savanna, Shafer 11704 (NY); Pinales Almácigos, Wright 1937 (G, HOLOTYPE; GH, MO, ISO-TYPES); without locality, Wright (MO, S; probably Wright 3685). ISLA DE Pinos: white-sand savannas, Santa Barbara, Alain & Killip 2120, 2146 (US), Killip 42666, 42695 (US); pinelands south of Santa Barbara, Killip 44112 (US); near Nueva Gerona, Curtiss 422 (G, L, NY, P), Jennings 648 (NY); pineland savannas, Río Júcaro region, Killip 42947 (US); savannas, Cemetario de Columbia, Killip 43586 (US); grassy pinelands, San Francisco de las Piedras, Killip & Swetland 41634 (US); barrens near Majagua River north of Los Indios, Jennings 408 (GH, NY); pinelands, San Pedro and vicinity, Britton & Wilson 14323 (NY); savannas between Santa Fe and San Juan, Killip 43926 (US).

This species characteristic of savannas and pinelands in western Cuba is easily distinguishable by its large floral and fruiting parts, as well as by the areolate pattern of its upper leaf-surface. Although the total area of the distribution of the species is not very large, it appears to be very common within this range and indeed ubiquitous in favorable localities. It is very similar in habit to *P. pentaphyllus* ssp. *pentaphyllus* and may be regarded as more or less coordinate in ancestry. Unlike *P. pentaphyllus*, *P. junceus* appears to prefer siliceous soil and is never found on calcareous substrates; this may partially account for its more restricted over-all range.

34. Phyllanthus pentaphyllus Wright ex Griseb. Goett. Nachr. 1865: 167. 1865.

A highly variable perennial herb becoming 0.2-3 dm. high, with the

main axis often abortive, the branches becoming clustered on a caudex and themselves more or less diffusely branching; flowering the first year, thus simulating an annual (and perhaps occasionally an annual in fact under difficult conditions); main stems erect or spreading, stramineous or greyish becoming dark brown in age, smooth or rarely minutely scabridulous, often somewhat channelled, c. 0.5–2 mm. thick; internodes (except in very depauperate plants) mostly 2–5 cm. long. Cataphylls: stipules



MAPS XV and XVI. Distribution of some species of subsect. Pentaphylli in Cuba.

ovate-triangular, mostly 0.9-1.3 mm. long, 0.5-0.7 mm. broad, acute to acuminate at the tip (or the lateral teeth sometimes obscuring the apex), entire to more commonly conspicuously dentate or lacerate, conspicuously auriculate at the base, dark reddish becoming blackish and indurate; blade linear-lanceolate. Deciduous branchlets (0.5-) 1-3 (-6) cm. long, 0.2-0.3 mm. thick, terete, furrowed, olivaceous or stramineous, smooth or rarely scabridulous, with 5-20 (-35) leaves; first internode (2.5-) 5-15 mm. long, second internode often very short and first two leaves hence subopposite, median internodes c. 0.5-1.5 (-2) mm. long. Leaves: stipules subpersistent, lanceolate, 0.4-0.8 (-1) mm. long, acuminate, olivaceous or sometimes reddish-tinged, entire, scarious (the proximal ones sometimes becoming reddish-black and indurate). Petioles 0.3-0.4 mm. long. Leaf-blades membranous to subcoriaceous, elliptic to mostly obovate or suborbicular, (1.5-) 2.5-7.5 (-8.5) mm. long, (0.75-) 1.5-4 (-5.5) mm. broad, mostly obtuse or rounded and often apiculate at the tip, acute to obtuse or rounded at the base; above smooth, deep green, the midrib inconspicuous; beneath smooth or minutely scabridulous, greyish or brownish, the midrib prominent, the laterals invisible to conspicuous and reticulate; margins plane or slightly reflexed, sometimes slightly thickened, smooth or roughened.

Monoecious (in the West Indies; only rarely and exceptionally dioecious); male flowers 5-25 in racemiform cymules, the scarious yellowish-

white bracteoles more or less persistent after fall of the flowers; female flowers solitary in the distal axils.

Male flower: pedicel mostly 0.4–0.8 mm. long. Calyx-lobes 5, subequal, rather strongly imbricate, obovate, (0.4-) 0.5–1 mm. long, (0.3-) 0.4–0.75 mm. broad, obtuse at the tip, entire to crenulate, yellowish and scarious, the midrib unbranched. Disk-segments 5, roundish or squarish, flat, subentire, not evidently glandular, c. 0.1–0.15 mm. across. Stamens 2; filaments connate beyond the middle into a column c. 0.2–0.3 mm. high; anthers short-stipitate or subsessile atop the column, discrete (rarely united at the base), c. 0.1–0.2 mm. long, 0.15–0.3 mm. broad; anther-sacs divergent, the slits confluent, dehiscing obliquely to horizontally; pollen grains finely reticulate, 21–25 μ long, 16–20 μ broad.

Female flower: pedicel becoming (0.8-) 1.2-2 (-2.7) mm. long, terete or sometimes obscurely angled, slender, tapering only slightly upwards, olivaceous, smooth. Calyx-lobes 5, subequal, elliptic to mostly obovate, becoming 0.8-1.2 mm. long and 0.5-0.75 mm. broad, subacute to rounded at the tip, entire or occasionally obscurely crenulate, herbaceous with broad whitish scarious margins, the midrib unbranched. Disk variable: cupuliform and merely angled, 5-lobed, or parted into 5 linear segments. Styles spreading or somewhat ascending, c. 0.15-0.2 mm. long, parted $(\frac{1}{4}-)$ $\frac{1}{3}$ to $\frac{1}{2}$ their length, the style-arms divergent, the slender tips recurving.

Capsule oblate, rounded, c. 1.7–1.9 mm. in diameter, smooth, stramineous or olivaceous, the veins obscure. Seeds acutely trigonous, 0.8–1 mm. long, 0.7–0.8 mm. radially and tangentially, light brown, with 6–8 delicate but often obscure slightly raised longitudinal striae on the back, transversely barred on the back with slightly hygroscopic epidermal cells.

Collected flowering and fruiting throughout the year.

This highly variable species has a broad range embracing most of the West Indies but with many lacunae as regards its local distribution. It shows close relationships to *P. junceus* on the one hand and to *P. pulverulentus* and *P. echinospermus* on the other; all four of these species have in common a more or less acaulescent habit which is associated with an unusual degree of development of branches from collateral buds, both at the cotyledonary and at subsequent nodes. The result is that the plants have clusters of rather wand-like stems either at the swollen end node of the original main axis or one of the branches.

Ecologically, *P. pentaphyllus* is well separated from *P. junceus* and *P. echinospermus* by its preference for calcareous habitats; but it is merely geographically isolated from *P. pulverulentus*, which grows on precisely the same sort of littoral coral platforms that *P. pentaphyllus* does. It is hardly surprising that of these three species related to *P. pentaphyllus*, the least distinctive is *P. pulverulentus*, which has the earmarks of a subspecies showing geographical replacement; but in the present treatment, *P. pulverulentus* is retained at specific rank because of its reasonably well-marked characters.

KEY TO THE SUBSPECIES

Leaves subcoriaceous, broadly obovate to suborbicular (1.2–1.7 times as long as broad), the lateral veins very obscure or invisible beneath; disk (at anthesis) 5-angled or shallowly and obtusely 5-lobed; plants stiffly erect. ssp. polycladus. Leaves membranous to chartaceous, more narrowly obovate (1.7–2.5 times as long as broad), the lateral veins and tertiary reticulum usually prominent beneath; disk of female flower deeply 5-lobed or parted into 5 linear segments; plants with usually more flexible, often spreading, stems ssp. pentaphyllus.

34a. Phyllanthus pentaphyllus ssp. pentaphyllus (PLATE XXI, figs. C-D).

Phyllanthus niruri ζ radicans Muell. Arg. Linnaea 32: 44. 1863; DC. Prodr. 15(2): 407. 1866.

Phyllanthus radicans (Muell. Arg.) Small, Fl. S.E. U. S. 692. 1903. Phyllanthus polycladus var. γ curassavicus Urb. Symb. Ant. 5: 384. 1908.

Perennial or sometimes appearing annual, stems smooth or rarely scabridulous, rather flexuous, upright or spreading. Deciduous branchlets (0.5–) 1–3.5 (–6) cm. long, with (5–) 8–25 (–35) leaves. Leaf-blades membranous or chartaceous, flexible or brittle, obovate to spathulate, sometimes quite narrow, (1.5–) 3–6 (–8.5) mm. long, (0.75–) 1–3.5 (–5) mm. broad, mostly 1.7–2.5 times as long as broad; lateral veins usually rather conspicuous beneath, a reticulum of delicate veinlets often visible; margins rather clearly demarcated, thicker than the blade, more or less roughened by projecting cell walls.

Monoecious (very rarely dioecious); proximal 0-2 axils barren, succeeded by 2-4 axils with cymules of (5-) 10-25 male flowers; cymule often with twin axes (the first branching being dichasial), or sometimes cristate and developing into a thick cluster of flowers.

Male flower: calyx-lobes entire, obovate, 0.4–0.7, mm. long, 0.3–0.5 mm. broad; staminal column c. 0.2–0.25 mm. high. Female flower: pedicel (0.8–) 1.2–2 (–2.7) mm. long; calyx-lobes 0.5–1.2 mm. long, 0.25–0.6 mm. broad; disk deeply 5-lobed or parted into 5 lanceolate to linear segments.

Type: Cuba, Pinar del Río, Santa Cruz, on rocks in the river, 8 April 1863, Wright 1938 ex p. (GOET, holotype; GH, MO, NY, S, US, isotypes). Wright's collection is a mixture of plants from at least two different localities; the citation of type locality is the result of matching the data on the Goettingen and Gray Herbarium specimens. The other locality, the label for which is also on the Gray Herbarium sheet, is Lagunillas, River San Sebastian, and is presumably also in Pinar del Río, although it has not been located on any map. There are two rather distinctive forms represented in the type collection, one with shorter branch internodes and monoecious inflorescences, the other with longer branch internodes and dioecious inflorescences (this latter form occurring on the New York and Stockholm sheets). Various circumstances suggest that the monoecious

form was collected at Santa Cruz and the dioecious form probably at Lagunillas, so that the nomenclatural type fortunately must be associated with the far more common monecious plant.

DISTRIBUTION: ssp. pentaphyllus comprises two varieties: var. pentaphyllus, which is very widespread in the West Indies, and var. floridanus, which is restricted to southern Florida (MAP X).

BAHAMAS. GREAT BAHAMA: pinelands, Eight Mile Rocks, Britton & Mills-paugh 2381 (F, NY). ELEUTHERA: Governor's Harbor and vicinity, sandy soil, Britton & Millspaugh 5514 (F, NY). Mariguana [Mayaguana]: 5 mi. west of Southeast Point, Wilson 7552 (F, NY).

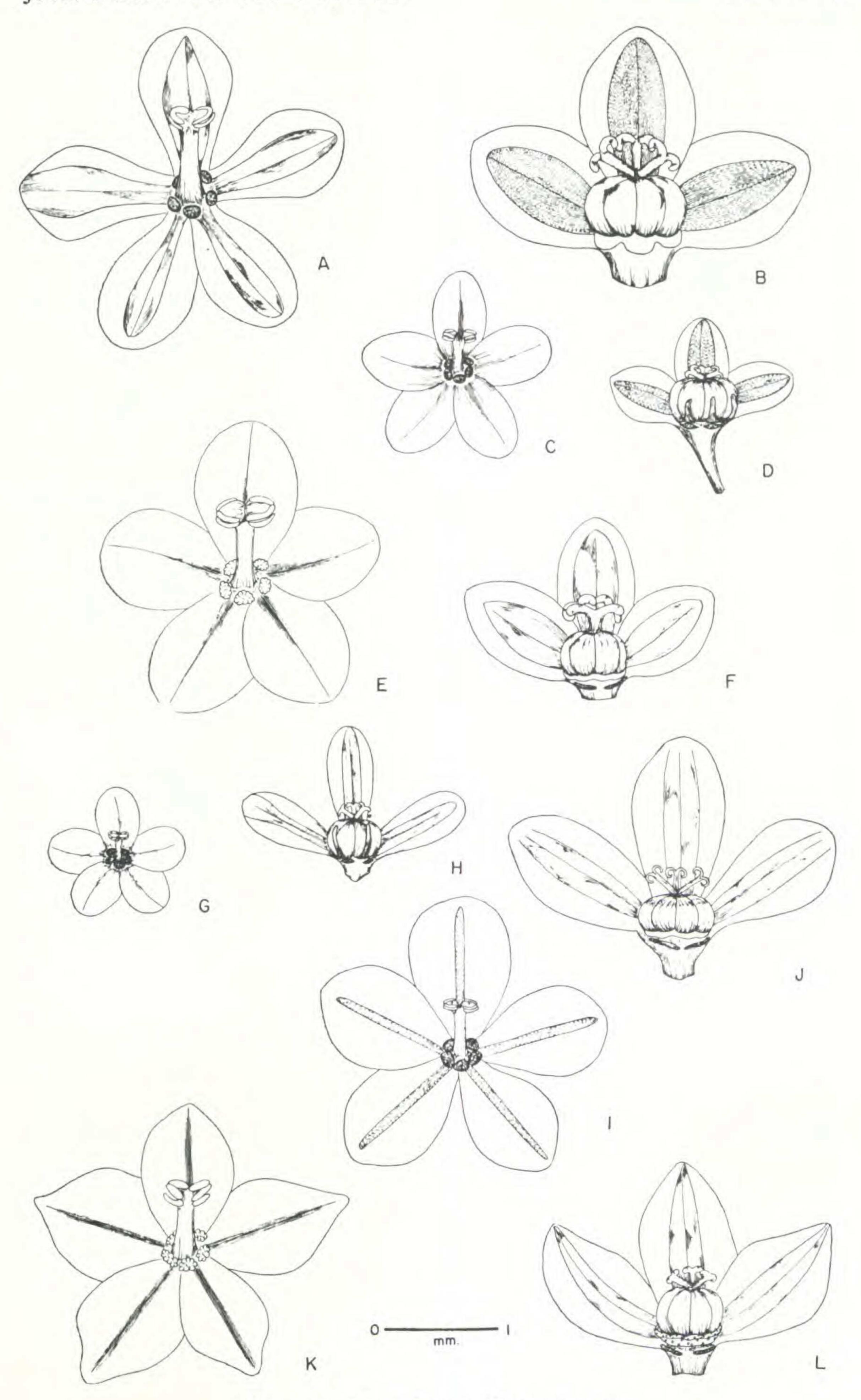
CUBA. PINAR DEL Río: Arroyo del Sumidero, dry rocks above the water, Shafer & León 13587 (NY); Pinar del Río City, Mateo Sanchez, moist places, Ekman 17933 (MICH, S); Sierra de los Organos, San Diego de Tapía, at the edge of the Río Maní-Maní, Ekman 12679 (S); La Cajálbana, La Mulata, Acuña (SV 18221); La Cajálbana, La Palma, Acuña & Alain (SV 15812); Santa Cruz, on rocks in the river, Wright 1938 ex p. (GOET, HOLOTYPE; GH, MO, NY, S, US, isotypes); River San Sebastian, Lagunillas, Wright 1938 ex p. (GH, and perhaps some of the other isotype sheets); bay of Mariel, Britton & Earle 7597 (F, NY), 7610 (NY, US); Mariel, Tinaja, towards Río Dominica, Ekman 12882 (S); without specific locality, Wright "48" (GOET, probably Wright 1938). ISLA DE PINOS: Nueva Gerona, near the marble quarry at the foot of Sierra Las Casas, on shaded rocks, Ekman 12571 (S). Habana: Havana, Hermann 62 (F, NY); Vedado, Ekman 149 (S); prope Morro in rupibus, Ekman 1164 (S); Playa de Jaimanitas, León 6294 (NY); Cabana Fortress, León 11396 (NY); Playa de Baracoa, León 8440 (NY); Cuabal de Jesus Maria near Minas, León 4781 (NY, SV). MATANZAS: Boca de Canasí, on limestone rocks, León 13172 (NY); coral rocks, playa, Matanzas,, Britton et al. 92 (NY); Matanzas, among bushes and grass near the bay, Wright "123" (GOET); Canimar, Otto 51 (W); shore of Matanzas Bay, limestone ledges near Canimar Bridge, Webster 4800 (GH). Las VILLAS: Trinidad Mountains, Hanabanilla Falls, rocky river bed, Britton et al. 4850 (F, NY).

HAITI. OUEST: Pte.-á-Raquettes, Ile Gonave, Ekman H8879 (S, US), Eyer-dam 272 (F, GH, NY, US).

DOMINICAN REPUBLIC. PUERTO PLATA: Sosúa, rock fissures on coral reef, Ekman H14481 (S). Barahona: sea-shore, Fuertes 1078 (A, F, GH, US); bei Paraíso, Fuertes 961 (A, NY, P, W).

PLATE XXI. Flowers of sect. Phyllanthus, subsect. Pentaphylli.

Figs. A-B. Phyllanthus junceus Muell. Arg. (male, Killip 43926 [US]; female, Killip 42947 [US]). Figs. C-D. Phyllanthus pentaphyllus Wright ex Griseb. ssp. pentaphyllus (male, Eyerdam 272 [GH]; female, Ekman 1164 [S]). Figs. E-F. Phyllanthus pulverulentus Urb. (male, Webster 3981 [GH]; female, Webster 3937 [GH]). Figs. G-H. Phyllanthus echinospermus Wright (Ekman 18131 [S]). Figs. I-J. Phyllanthus selbyi Br. & Wils. (Britton & Wilson 14157 [MO]). Figs. K-L. Phyllanthus imbricatus Webster (Britton & Wilson 14192 [GH]).



Webster, West Indian Phyllanthus

CURAÇÃO. CURAÇÃO: P. E. Benzon (C); Ft. Nassau, calcareous land, Suringar 2 (L, type collection of P. polycladus var. curassavicus); limestone rocks near Willemstad, Britton & Shafer 2948 (F, US). Bonaire: Boldingh 7278 (C, L).

Although this very polymorphic population could perhaps be subdivided further into varieties, the present broad circumscription seems the most practicable. Actually, the only additional entity recognized within ssp. pentaphyllus, var. floridanus, is very weakly defined; it differs from var. pentaphyllus mainly in its dioecious inflorescence, but dioecious individuals do occur (though rarely) in the Cuban population. Consequently, if any taxonomic adjustments are made, the result may prove to be the deletion of the two varieties now existing rather than the erection of additional ones.

The distribution of ssp. pentaphyllus appears to be curiously disjunct, and it appears doubtful that future collecting will appreciably narrow the gaps. It might be supposed that such a distant station as that in Curaçao might show appreciable taxonomic differences, but there do not appear to be any significant differences between the plants from the Dutch islands and those from Cuba. The absence of ssp. pentaphyllus from eastern Cuba may be accounted for by its replacement by P. pulverulentus, and its apparent rarity in Hispaniola may simply reflect inadequate collecting; but the spotty distribution in the Bahamas is more difficult to explain. The plants from the Lesser Antilles (Guadeloupe), which show a much closer approach to ssp. pentaphyllus than one would expect from their proximity to ssp. polycladus, also pose a problem in relationships that cannot be resolved at this time.

34b. Phyllanthus pentaphyllus ssp. polycladus (Urb.) Webster, Contr. Gray Herb. 176: 56. 1955. (PLATE XXII, fig. C).

Phyllanthus polycladus Urb. Symb. Ant. 1: 333. 1899.

Phyllanthus polycladus B guadeloupensis Urb. ibid.

Perennial, woody at the base, branches mostly stiffly erect (at least below). Deciduous branchlets 0.7–1.5 (–2.7) cm. long, with (4–) 5–12 leaves. Leaf-blades subcoriaceous, broadly ovate to suborbicular, 2.5–5 (–6) mm. long, 2–4 mm. broad, mostly 1.2–1.7 times as long as broad; lateral veins inconspicuous or invisible; margins not clearly demarcated except by color (scarcely thicker than the blade), smooth.

Monoecious, the proximal 0-1 nodes barren, the succeeding 2-4 nodes with racemiform male cymules.

Male flowers: calyx-lobes more or less crenulate, broadly obovate, 0.7–1 mm. long, 0.65–0.75 mm. broad; staminal column 0.2–0.35 mm. high. Female flower: pedicel 0.8–1.8 mm. long; calyx-lobes 0.8–1.2 mm. long, 0.5–0.7 mm. broad; disk cupuliform and merely 5-angled or shallowly and obtusely 5-lobed.

Type: Puerto Rico, Sintenis 3440.

DISTRIBUTION: Puerto Rico and the Lesser Antilles (MAP X).

PUERTO RICO. Mayaguez: limestone east of Guayanilla. Britton & Britton

9141 (F, NY); prope Guanica in rupibus litoralibus ad salinas, Sintenis 3440 (NY, LECTOTYPE; A, F, GH, L, MO, NY, P, US, W, ISOTYPES); rocky coastal thicket, Guanica and vicinity, Britton & Shafer 1912 (NY, US); salinas de Guanica, Britton, Cowell, & Brown 4913 (F, NY, US). Ponce: Cayo Muertos, coastal limestone rocks, Britton, Cowell, & Brown 4998 (F, MO, NY, US); crevices of rocks near Ponce, Underwood & Griggs 696 (NY, US). Humacao: Icacos Cay, limestone rocks, Britton 7171 (NY, US).

LESSER ANTILLES. Anegada: rocky plain near settlement, Britton & Fishlock 1000 (F, MO, NY, US). Guadeloupe: Vieux-Fort, champs de manioc, endroits secs, sablonneux, Duss 209 (P); hauteurs de Vieux-Fort, abondant dans le terrain rocailleux et sec, Duss 2443 (F, GH, NY, US).

A collection purportedly from St. Thomas, in the Virgin Islands (*Fried-richsthal 383* [W]), is not listed above because its characters on the whole agree better with ssp. *pentaphyllus* and also because it seems rather unlikely that the plant has not been recollected on such a comparatively well-known island as St. Thomas. It must be granted, however, that since the plants from Guadeloupe also approach ssp. *pentaphyllus*, there is a possibility that the populations east of Puerto Rico may ultimately prove not to belong to ssp. *polycladus*; in such an event, Friedrichsthal's record would no longer be surprising. A careful search for *P. pentaphyllus* on St. Thomas is highly desirable.

Two collections from Indiera Fria, Maricaco, Aquadilla Province, Puerto Rico (Stevens & Hess 3328, 3347 [NY]), are too fragmentary to be positively identified, but may represent an aberrant form of ssp. polycladus. They differ in having branchlets up to 4.2 cm. long with narrow leaves, and in being apparently dioecious. Additional specimens will have to be procured from this population in order to ascertain its exact affinity.

In his original publication of *P. polycladus*, Urban merely referred it to sect. *Euphyllanthus* and remarked it as distinct by its two stamens, without discussing its relationships. Subsequently (on labels) he applied the name *P. polycladus* to individuals of ssp. *pentaphyllus* from Cuba and Hispaniola, so that evidently he did not appreciate the fact that Wright had already described the species nor that any real differences existed between the plants of Cuba and those of Puerto Rico. Careful study of all available collections demonstrates, however, that the species may be divided into two subspecies which are so distinctive that they might appear to merit specific rank. The intermediate nature of the plants from Guadeloupe suggests on the contrary that the two populations have not yet attained specific distinctiveness, and confirmation of Friedrichsthal's collection from St. Thomas would strengthen this point of view. In any event, there appears to be no necessity for designating or recognizing any further subspecific taxa, such as Urban's var. *guadeloupensis*.

35. Phyllanthus pulverulentus Urb. Symb. Ant. 9: 192. 1924. (PLATE XXI, figs. E-F).

Suffruticose perennial c. 1–3 dm. high, copiously branching from a woody base; branches erect or spreading, terete, stramineous or brownish, smooth

or minutely scabridulous, c. 0.5-0.6 mm. thick; internodes c. 0.5-3 (-4.5) cm. long. Cataphylls: stipules deltoid-ovate, 0.8-1.2 mm. long, 0.6-0.9 mm. broad, acute to acuminate at the tip, conspicuously auriculate at the base, entire to conspicuously dentate (sometimes distally several-toothed, with a definite apex), becoming reddish-black and indurate; blade linearlanceolate, 0.5-0.8 mm. long. Deciduous branchlets (1-) 1.5-3 (-4) cm. long, 0.2-0.3 mm. thick, subterete, olivaceous, smooth to densely scabridulous, with mostly 7-25 leaves; first internode (1-) 1.5-7 (-8) mm. long, median internodes 1-3 (-4) mm. long. Leaves: stipules more or less deciduous, lanceolate, c. 0.5-0.9 mm. long, acuminate, entire, yellowish, scarious. Petioles 0.25-0.5 mm, long. Leaf-blades firmly chartaceous, scabridulous on both sides but more conspicuously so beneath, elliptic or oblong to obovate or sometimes suborbicular, c. (2.5-) 3-5 (-6) mm. long, (1.5-) 2-3 mm. broad, obtuse to rounded or occasionally subacute at the tip, obtuse or rounded at the base; above greyish-green, the midrib obscure, the laterals invisible; beneath yellowish-green, the midrib raised, the laterals obscure or invisible; margins somewhat thickened, plane, scabridulous.

Monoecious or subdioecious. Branchlets of 3 types: (1) bisexual, the proximal 1–3 nodes barren, the succeeding 3–9 nodes with cymules of male flowers, the distal with solitary female flowers; (2) predominantly male, with no barren nodes, the proximal 10–14 nodes with male flowers, the 1 or 2 distal nodes with or without female flowers; and (3) female, never with any male flowers, the proximal 5–6 nodes barren. Male cymules with c .5 or 6 flowers, monochasial or dichasial at the first branching; bracteoles yellowish-white, scarious, persistent.

Male flower: pedicel c. 0.5–0.8 mm. long. Calyx-lobes 5, subequal, obovate, 0.9–1.2 mm. long, 0.6–0.9 mm. broad, obtuse or rounded at the tip, entire, yellowish-scarious, the midrib usually unbranched (that of larger lobes occasionally with a few obscure branches). Disk-segments 5, plane or concave, roundish, c. 0.2 mm. across, subentire or crenulate, not conspicuously glandular. Stamens 2 (rarely 3); filaments completely united into a column (0.3–) 0.4–0.5 mm. long; anthers sessile atop the column, more or less fused back-to-back, often unequal, c. 0.2 mm. long and 0.25–0.3 mm. broad; anther-sacs widely divergent, the slits confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 21–26 μ long, 16–20 μ broad.

Female flower: pedicel becoming (0.7–) 1.2–1.8 (–2.2) mm. long, olivaceous, terete, gradually dilated from the base, smooth. Calyx-lobes 5 (rarely 6), subequal, obovate, c. 1.2–1.7 mm. long, 0.8–1.2 mm. broad, rounded at the tip, entire, with yellowish-scarious margins, the midrib branched but the laterals quite obscure. Disk shallowly cupuliform, thin, the 5-angled rim undulate or crenulate. Styles spreading or ascending, c. 0.3–0.4 mm. long, parted c. ½ their length, the branches divergent, the slender blunt tips recurved.

Capsule oblate, c. 2.2–2.4 mm. in diameter, shallowly sulcate, smooth, yellowish-brown, not veiny. Seeds trigonous, c. 1–1.1 mm. long, 0.85–

0.9 mm. radially and tangentially, pale to dark brown, with c. 12-14 delicate longitudinal striae and transversely barred by non-hygroscopic epidermal cells.

Type: Cuba, Ekman 7736.

DISTRIBUTION: Coastal terraces, southeastern Oriente Province, Cuba (Map X).

CUBA. ORIENTE: between Santiago de Cuba and El Morro, on coral, 25 Sept. 1916, Ekman 7736 (S, HOLOTYPE); limestone rocks at El Morro, steep slopes facing the sea, 6 July 1924, Ekman 19197 (MICH, NY, S); vicinity of Guantánamo, limestone hills along the coast between Escondido Bay and the Río Yateras, 28 July 1951, Webster 3937 (GH, MICH, NY); coastal limestone terrace between the Río Yateras and Baitiquirí, 31 July 1951, Webster 3981 (GH, MICH, NY).

This species, with its rigid stems and leaves, appears to be a local woodier representative of the widespread Caribbean species P. pentaphyllus, which it indeed replaces in Oriente. It would be possible to regard P. pulverulentus as merely a subspecies of the wide-ranging plant, and the disposition made above of the Puerto Rican ssp. polycladus might appear to justify such a point of view. However, although the criteria are admittedly subjective, the Oriente population, with its larger male flowers and distinctive leaves, appears to be well-marked enough to stand at the specific level, whereas the Puerto Rican plant does not.

36. Phyllanthus echinospermus Wright, Anal. Acad. Ci. Habana 7: 108. 1870. (PLATE XXI, figs. G-H).

Phyllanthus minimus Wright, idem 108-109.

Slender depauperate herb, flowering precociously and appearing as if an annual, but at length perennial, the primary axis becoming abortive or confounded with numbers of more or less procumbent branches c. 2-5 (-10) cm. long, 0.3-0.6 (-0.9) mm. thick, smooth, terete, light brown, with internodes c. (0.5-) 1-1.5 (-2) cm. long. Cataphylls: stipules deltoidovate, 0.8-1.1 mm. long, 0.4-0.6 mm. broad, acute, auriculate at the base, entire or somewhat denticulate, reddish-brown becoming dark brown or blackish and indurate. Deciduous branchlets 1-2.5 cm. long, 0.15-0.2 mm. thick, smooth, terete, reddish-brown, with c. 10-15 leaves; first internode mostly 3-7 mm. long, median internodes c. 0.8-1 mm. long. Leaves: stipules linear-lanceolate, 0.5-1 mm. long, 0.15-0.2 mm. broad, attenuateacuminate, reddish with narrow whitish scarious margins. Petioles c. 0.3-0.4 mm. long. Leaf-blades thin, elliptic or elliptic-obovate, (1.5-) 2-4 mm. long, 1-2 mm. broad, obtuse or rounded at the tip, obtuse often somewhat inequilateral at the base, minutely scabridulous on both sides (but more conspicuously so beneath); above green or reddish-tinged, midrib impressed and rather inconspicuous, the laterals invisible; beneath often reddish, the midrib conspicuous and raised, the laterals scarcely or not at all visible; margins plane, slightly thickened, smooth, more or less reddish-tinged.

Monoecious; proximal (0-) 1-3 (-4) nodes barren; succeeding (1-) 2-4 (-6) nodes with racemiform cymules (less than 0.5 mm. long) of 3-5 male flowers; distal axils with solitary female flowers.

Male flower: pedicel 0.3–0.7 mm. long. Calyx-lobes 5, suborbicular, equal, c. 0.4–0.5 mm. long, 0.25–0.4 mm. broad, obtuse or rounded at the tip, entire, yellowish, subhyaline, obscurely carinate along the unbranched midrib. Disk-segments 5, roundish, thin, more or less entire, c. 0.1 mm. across. Stamens 2; filaments completely connate into a column 0.15–0.2 mm. high; anthers sessile atop the column, c. 0.2 mm. long and 0.3 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing more or less horizontally; pollen grains finely reticulate, 21–24 μ long, 16–19 μ broad.

Female flower: pedicel (0.5–) 0.9–1.2 mm. long, more or less angled and reddish-tinged. Calyx-lobes 5, becoming definitely spathulate in fruit, 0.9–1.2 (–1.5) mm. long, 0.4–0.5 (–0.6) mm. broad, rounded at the tip, entire, the scarious margins broader than the narrow herbaceous midstrip, dorsally carinate along the unbranched midrib, often conspicuously reddish-tinged. Disk parted into 5 distinct linear, subulate segments c. 0.25–0.3 mm. long. Styles ascending, rather fleshy, c. 0.15–0.2 mm. long, bifid, the branches reflexed.

Capsule oblate, rounded-trigonous, c. 1.4–1.5 mm. in diameter, smooth, stramineous or brownish, the veins completely obscure. Seeds trigonous, 0.6–0.7 mm. long, 0.4–0.55 mm. radially and tangentially, brownish, transversely barred with hygroscopic epidermal cells which recurve as clavate brown-stained trichomes (the longitudinal striae completely obscure).

Collected in November and December.

Type: Cuba, Pinar del Río, Wright 3687.

DISTRIBUTION: endemic to the lagoon area, western Pinar del Río (MAP XVI).

CUBA. Pinar del Río: Laguna Jovero, sandy soil, Shafer 10774 (NY); Laguna Jovero to Laguna del Bufeo, in wet sand, Shafer 10996 (NY); Laguna Santa Barbara, in the Paurotis-belt, sandy places, Ekman 18112 (S); Laguna Alcatraz Grande, in white sand, Ekman 18131 (S); Laguna de la Máquina de Tarafa, Wright 3686 (F, GH, NY, P, US;type collection of P. minimus), 3687 (GH, Lectotype; F, NY, US, Isotypes); same locality, steep sides of a small brook, Ekman 17903 (S); Pinar del Río City, between Laguna de la Máquina and Laguna de Junio, in somewhat moist places, Ekman 17907 (S).

This species, which is one of the most diminutive in the West Indies, is easily recognizable by its leaves scabridulous on both sides, its spathulate usually reddish-tinged fruiting calyx-lobes, and its linear female disk-segments. Its habit is precisely like that of very depauperate individuals of *P. pentaphyllus*, and it does indeed appear to be closely related to that species. Ecologically, the two are well separated, since *P. echinospermus* is found on sand usually at the edge of lagoons, while *P. pentaphyllus* is a calciphile growing in stream-beds or along the seacoast.

Specimens of the proposed species P. minimus, described by Wright from

individuals collected at the same locality, differ in no way from *P. echinospermus* except that they represent very young individuals, some of which are flowering at the third or fourth branchlet while the cotyledons are still attached. In combining the two species, it seems appropriate to conserve the epithet *echinospermus* for the aggregate concept, since the hygroscopic cells of the very small seed are a characteristic feature of the species.

37. Phyllanthus selbyi Br. & Wils. Mem. Torr. Bot. Club 16: 74, 1920. (PLATE XXI, figs. I–J; PLATE XXII, fig. D).

Erect perennial herb (but flowering first year and then appearing as if annual) with dendroid form, the main stem sparingly to copiously branching above, becoming 2-4 dm. high, terete, rather woody, with bark becoming blackened and fissured in age; internodes of main stem mostly 0.5-2 cm. long. Cataphylls: stipules ovate-lanceolate, 1.2-1.5 mm. long, 0.5-0.7 mm. broad, acuminate, auriculate at the base, entire or conspicuously dentate, becoming blackish and indurate; blade linear-lanceolate, 0.6-1.1 mm. long, 0.1-0.15 mm. broad. Deciduous branchlets (1-) 2-3 (-3.5) cm. long, 0.15-0.3 mm. broad, terete, smooth, reddish-brown or stramineous and more or less pruinose, with mostly (15-) 20-30 (-35) leaves; first internode c. 3.5-6 mm. long, median internodes 0.6-1.3 mm. long. Leaves: stipules linear-lanceolate, 0.5-0.7 mm. long, 0.15-0.2 mm. broad, acuminate, distally scarious-tipped, reddish-tinged with entire whitish scarious margins. Petioles c. 0.2-0.3 mm. long. Leaf-blades rather thick, elliptic or oblong to obovate, 2-3 mm. long, 1-1.8 mm. broad, acute or obtuse at the tip, rounded at the base; pale green and somewhat pruinose above and below, the veins invisible except for the rather faint midrib; margins plane, more or less reddish-tinged, smooth or sometimes slightly roughened.

Dioecious or subdioecious; male branchlets normally with the proximal 6–10 nodes barren, succeeding ones with racemiform cymules (up to 0.5 mm, long) of 3–7 flowers; female branchlets with the proximal 10–17 nodes barren, followed by solitary flowers; occasional male branchlets pro-

ducing a single distal female flower.

Male flower: pedicel 0.4–0.7 mm. long. Calyx-lobes 5, elliptic to obovate, unequal, the longer c. 0.7–1.2 mm. long and 0.6–0.75 mm. broad, the shorter c. 0.6–0.9 mm. long and 0.5–0.7 mm. broad, obtuse or rounded at the tip, yellowish-scarious except for the narrow herbaceous area along the dorsally carinate unbranched midrib. Disk-segments 5, transversely elongate, not conspicuously glandular, c. 0.1–0.2 mm. across. Stamens 2; filaments completely united into a column 0.3–0.4 mm. high; anthers sessile atop the column, 0.2–0.3 mm. long, 0.25–0.4 mm. broad; anther-sacs divergent, the slits apically confluent, dehiscing obliquely; pollen grains finely reticulate, 22–24 μ long, 18–20 μ broad.

Female flower: pedicel (0.6–) 1–1.4 mm. long, terete, smooth, olivace-ous, angled. Calyx-lobes 5 (rarely 6), elliptic to obovate, subequal, 1–1.4 mm. long, 0.6–0.8 mm. broad, obtuse or rounded at the tip, with yellowish scarious margins broader than the greenish midstrip, dorsally carinate

along the unbranched midrib. Disk variable, usually deeply 5-lobed, sometimes merely with 3-5 notches, the thin lobes squarish or triangular. Styles ascending, 0.25-0.35 mm. long, bifid ¼ their length or less, the very short unthickened branches recurved.

Capsules not seen entire; valves stramineous, the veins obsolete. Seeds sharply trigonous, c. 0.9 mm. long, 0.65–0.75 mm. radially and tangentially, dark brown, the longitudinal striae very obscure or invisible, transversely barred by hygroscopic cells which project as slightly clavate setae when moistened.

Collected in flower or fruit November to May; perhaps flowering throughout the year.

Type: Cuba, Isle of Pines, Britton et al. 14157.

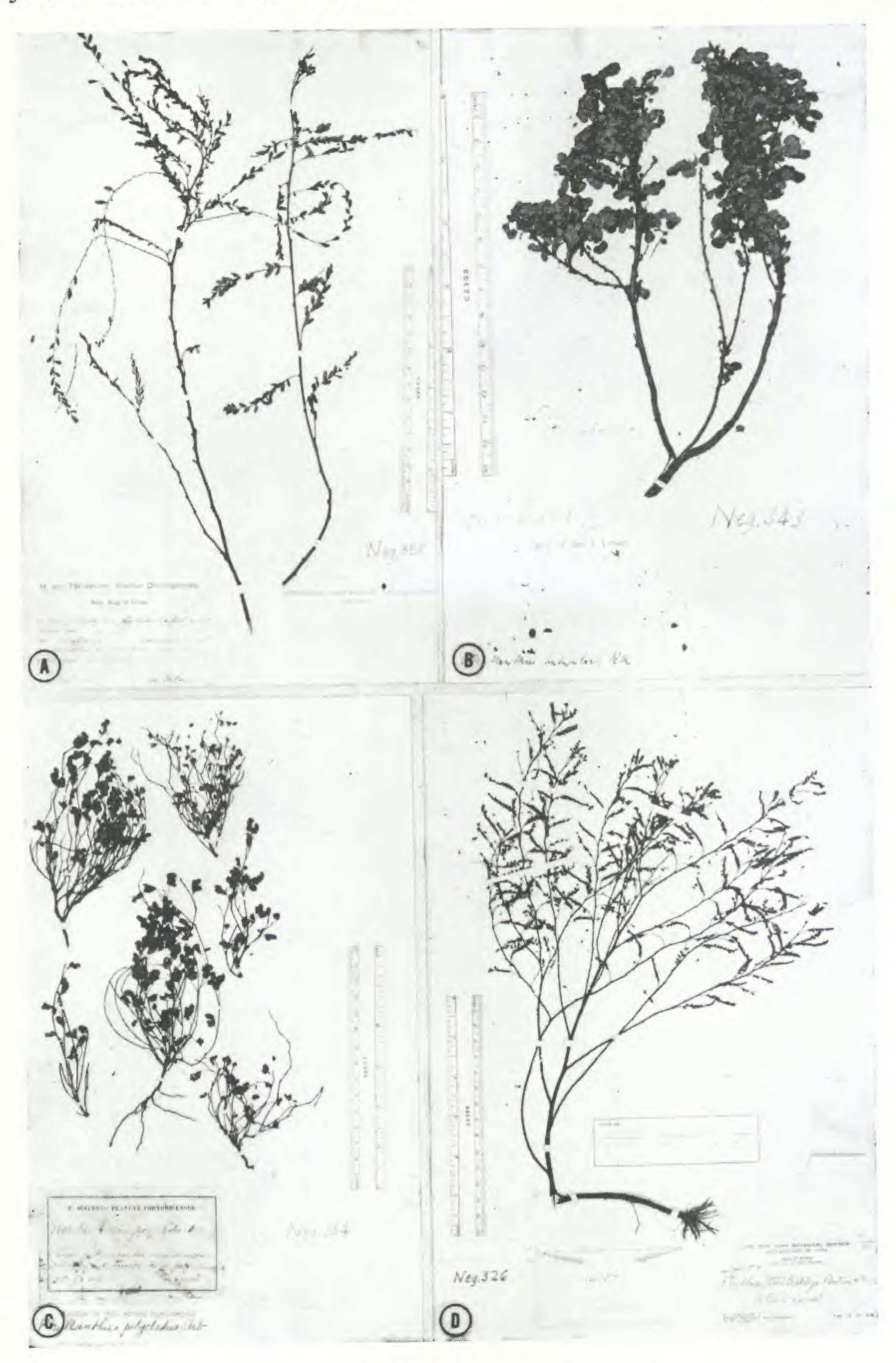
DISTRIBUTION: endemic to the Isle of Pines (MAP XVI).

CUBA. ISLA DE PINOS: Santa Barbara, Alain & Killip 2120, Killip 42666 (US); between San Francisco de las Piedras and Cerro la Canada, Killip 44633 (US); between Mina de Oro and Playa del Soldado. Killip 43896 (US); Los Indios, Alain & Killip 2174 (US), Ekman 12159 (S); Siguanea, Killip 44055 (US); San Pedro and vicinity, Britton, Wilson, & Selby 14157 (NY, HOLOTYPE; F, GH, MO, US, ISOTYPES); Las Tunas rivulet, León & Marie-Victorin 17892 (MICH).

This species, characterized by its resemblance to a miniature tree, is strikingly microphyllous, like many of its neighbors on the white sands of the Isle of Pines. Occasionally individuals of P. selbyi may produce a few branches from near the base; and in a collection from Santa Barbara (alkali flats on white sand, Ekman 12063 [NY, S]), not enumerated above, the plants are copiously branched from a basal caudex and, at first sight, appear completely different from P. selbyi. Urban proposed on the basis of this collection a new species, P. pinosius, supposedly differing from P. selbyi in having two stamens instead of three. Urban was here misled by Britton and Wilson, who either erred in recording the stamen number of P. selbyi or else happened to dissect by chance a rare flower with three stamens (only two stamens were observed in repeated dissections of the flowers of the species). The Ekman collection differs not only in its habit but also in its longer (1.5-1.8 mm.) female calyx-lobes; but in most other respects it is essentially identical with typical individuals of P. selbyi. Since P. selbyi may sometimes produce basal branches as well, it seems probable that the plants described as P. pinosius are outstanding because of some environmental modification rather than any significant genetic diversity.

PLATE XXII. Types of growth form in sect. Phyllanthus.

Fig. A. Phyllanthus leptoneurus Urb. (Turckheim 3187 [BR, lectotype]). Fig. B. Phyllanthus fadyenii Urb. (Macfadyen [K, holotype]). Fig. C. Phyllanthus pentaphyllus Wright ssp. polycladus (Urb.) Webster (Sintenis 3492 [US]). Fig. D. Phyllanthus selbyi Br. & Wils. (Britton, Wilson, & Selby 14157 [NY, holotype]).



Webster, West Indian Phyllanthus

The only species very closely related to *P. selbyi* is *P. imbricatus*, which is clearly a further reduced derivative species with a distribution even more narrowly restricted on the Isle of Pines. Evidently related also is *P. echinospermus*, which has a similar hygroscopic seed-coat, and which occupies somewhat similar habitats in western Pinar del Río.

38. Phyllanthus imbricatus Webster, Contr. Gray Herb. 176: 56. 1955. (PLATE XXI, figs. K-L).

Phyllanthus nanus Millsp. Bull. Torr. Bot. Club 43: 464–465. 1916; non P. nanus Hook. f. Fl. Br. Ind. 5: 298. 1887.

Diminutive perennial herb; branches (0.5-) 1-2 (-5) cm. long, clustered on a caudex, usually prostrate and more or less buried in sand, sometimes considerably ramified, bearing branchlets above-ground at the tips, smooth and reddish-brown, above, becoming blackened in age; internodes c. 0.1-0.8 cm. long, 0.5-1 mm. thick. Cataphylls: stipules triangular-ovate, 1-1.3 mm. long, 0.7-1 mm. broad, acuminate, auriculate at the base, entire or the auricle toothed, becoming blackened and indurate and persisting on underground parts; blade linear-lanceolate, 0.7-1.1 mm. long, 0.15-0.2 mm. broad. Deciduous branchlets mostly 1-2 cm. long, 0.2-0.3 mm. thick, angled, smooth, stramineous or reddish-brown, with mostly 10-25 (-35) leaves; first internode mostly 4-7 mm. long, subsequent internodes only 0.3-0.9 mm. long, usually only half the length of the leaves, which thus overlap extensively. Leaves: stipules linear-lanceolate, 0.6-1 mm. long, 0.2 mm. broad, acuminate, stramineous with brownish tips, scarious (those at the proximal nodes often becoming indurate). Petioles 0.2-0.25 mm. long. Leaf-blades thick, ovate, 1.5-2 (-2.5) mm. long, 1.1-1.8 mm. broad, obtuse or subacute at the tip, cordate or subcordate at the base, pruinose, smooth or obscurely alveolate on both sides, the veins invisible above and below except for the faint midrib; margins somewhat thickened, plane, smooth or minutely roughened, sometimes reddish-tinged.

Monoecious or dioecious; proximal (3-) 5-10 (-12) nodes barren, succeeding nodes with cymules of 2-7 male flowers or solitary female flowers; bisexual branchlets entirely male except for 1 or 2 distal female flowers.

Male flower: pedicel only 0.2–0.3 mm. long. Calyx-lobes 5, elliptic, unequal, the longer c. 1.2–1.5 mm. long and 0.7–1 mm. broad, the shorter 0.9–1 mm. long and 0.5–0.7 mm. broad, rounded at the tip, yellowish and scarious except for the olivaceous dorsally carinate midstrip along the unbranched midrib. Disk-segments 5, squarish, c. 0.2 mm. across, conspicuously papillate-rugose. Stamens 2 (sometimes a rudimentary third anther developed); filaments completely connate into a column c. 0.2 mm. high; anthers sessile atop the column, c. 0.25 mm. long. 0.3–0.4 mm. broad; anther-sacs with apically confluent slits, dehiscing horizontally or somewhat obliquely; pollen grains finely reticulate, c. 21–24 μ long, 17–19 μ broad.

Female flower: pedicel only 0.2–0.3 mm. long. Calyx-lobes 5, elliptic (or becoming obovate in fruit), subequal, 1.2–1.5 mm. long, 0.6–0.8 mm. broad, narrowed to an obtuse or subacute tip, with yellowish scarious mar-

gins as broad as or broader than the olivaceous midstrip, dorsally carinate along the unbranched midrib. Disk undivided, 5-angled, obscurely and minutely crenulate. Styles free, ascending, c. 0.2 mm. long, reddish-tinged at first, bifid, the unthickened branches recurved.

Capsule c. 1.5 mm. in diameter, smooth, brownish-tinged, the veins completely obscure. Seeds sharply trigonous, 0.8–0.85 mm. long, 0.6–0.65 mm. radially and tangentially, dark brown, with 3 or 4 very inconspicuous longitudinal striae and many fine presumably hygroscopic barred epidermal cells on the back.

Type: Isle of Pines, Britton, Britton, & Wilson 14192.

DISTRIBUTION: endemic to the white sand areas, southwestern coast of the Isle of Pines (MAP XVI).

CUBA. ISLA DE PINOS: white-sand savannas, Los Indios, 27 Dec. 1951, Alain & Killip 2205 (US); same locality, 13 Feb. 1916, Britton, Britton, & Wilson 14192 (F, HOLOTYPE; GH, US, ISOTYPES); same locality, 8 Nov. 1920, Ekman 12144 (S).

This pygmaean species, with its prostrate partially buried stems and very short branchlets with small closely overlapping cordate leaves, is vegetatively the most highly specialized species of subsect. *Pentaphylli*. It is also one of the most narrowly endemic in range, since it does not appear to occur anywhere except in the white sands area of the Los Indios region, whereas its sister species *P. selbyi* is distributed much more widely in the Isle of Pines. It seems reasonable to regard *P. imbricatus* as a more or less dwarfed derivative of *P. selbyi*, for the close affinity between the two is very apparent. Nevertheless, *P. imbricatus* is unquestionably a perfectly distinct species which is easily distinguished from *P. selbyi* both by its habit and by its subsessile flowers, the male with papillate disk-segments.

Subgenus V. Eriococcus (Hassk.) Croiz. & Metc. Jour. Arnold Arb. 23: 32. 1942.

Eriococcus Hassk. in Hoeven & De Vriese, Tijdschr. 10: 143. 1843.

Subshrubs or shrubs with phyllanthoid branching; monoecious. Male flower: calyx-lobes 4–6, entire to conspicuously lacerate; disk cupuliform or of distinct segments; stamens 2 or 3, filaments connate; anthers dehiscing vertically to horizontally; pollen grains globose, porate. Female flower: calyx-lobes 4–6; disk patelliform to urceolate; ovary of 3–8 carpels, smooth or hirsute; styles bifid or entire, free or connate. Fruit capsular; seeds smooth.

In addition to the typical section *Eriococcus*, this entirely Old World subgenus includes sects. *Emblicastrum*, *Eriococcodes*, and *Scepasma*. These latter three sections, all monotypic when established, are open to the suspicion that they represent merely individual species with striking "key" characters; a recasting of subg. *Eriococcus* along phylogenetic lines may result in radical changes in the circumscription of the constituent taxa.

The majority of the species of subg. *Eriococcus* may be easily recognized by virtue of their lacerate calyx-lobes, distinctive androecium of two stamens, and porate pollen grains. The pollen has been examined in relatively few species, however, and should be checked in any whose exact affinities are being considered.

Sect. 12 Eriococcus (Hassk.) Muell. Arg. Linnaea 32: 46. 1863; DC. Prodr. 15(2): 420. 1866.

Eriococcus Hassk. in Hoeven & De Vriese, Tijdschr. 10: 143. 1843.

Reidia Wight, Icon. Pl. Ind. Or. 5(2): 27. pls. 1903, 1904. 1852.

Epistylium sect. Eriococcus (Hassk.) Baill. Etud. Gen. Euphorb. 648. 1858.

Shrubs with phyllanthoid branching, the stems often hirsutulous with reddish hairs. Monoecious; cymules unisexual. Male flower: calyx-lobes 4, decussate, margins more or less lacerate; disk-segments 4, large, petaloid; stamens 2, filaments connate; anthers dehiscing horizontally; pollen grains porate. Female flower: calyx-lobes 4–6, more or less fimbriate or lacerate along the margins; disk cupuliform; ovary of 3 carpels, smooth [in West Indian species]; styles more or less free, spreading, bifid.

Type species: Eriococcus gracilis Hassk. [= Phyllanthus gracilipes (Miq.) Muell. Arg.].

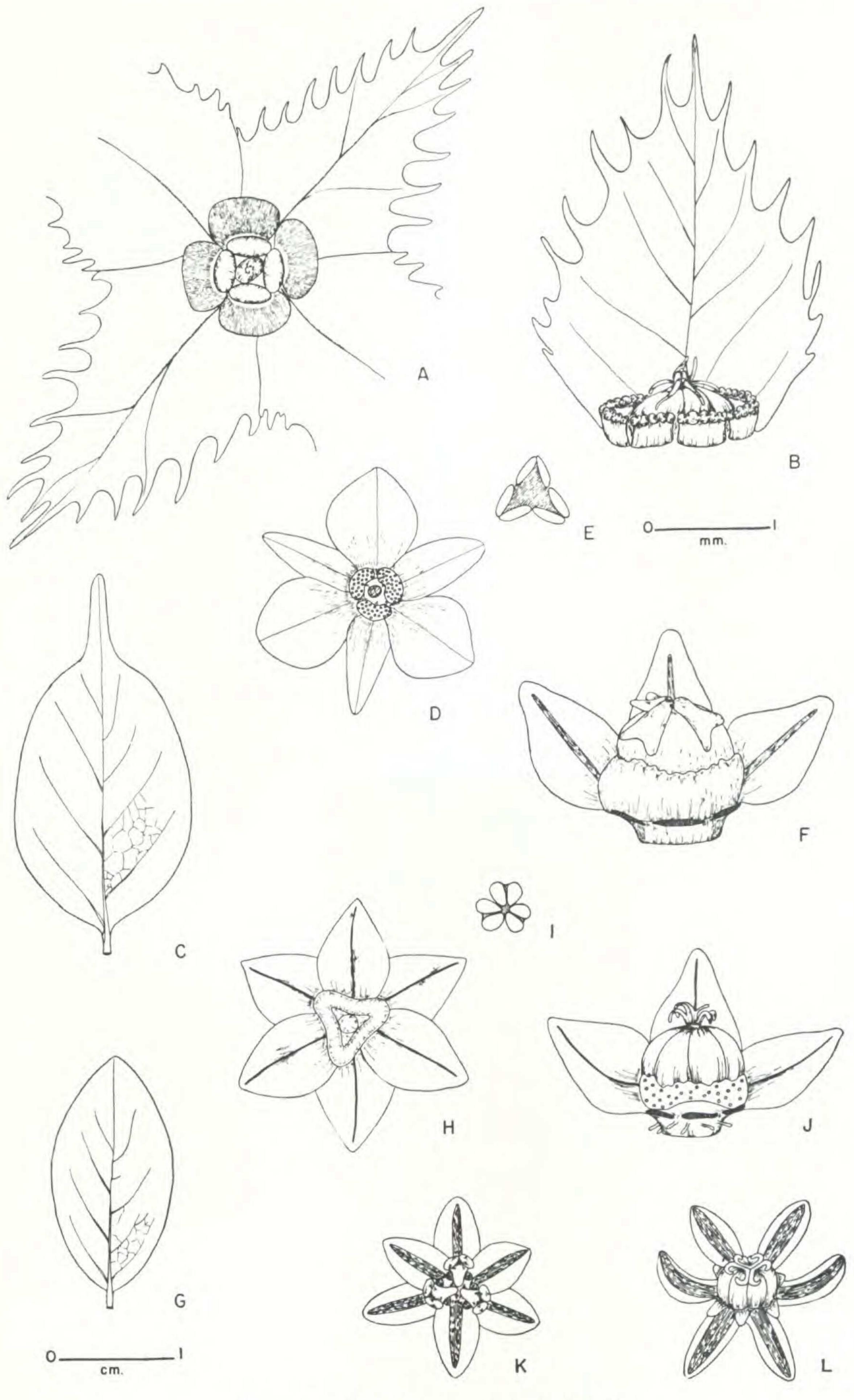
Section *Eriococcus* is an entirely Asiatic group of about 25 species which extend from southern India and Ceylon to Malaysia and the Philippines. Although it is evidently a natural group, its limits are rather hard to define, for the fimbriate calyx-lobes and vestite ovary of the type species do not occur in all of its relatives. There do not appear to be any close relatives of the section in the New World; although some of the species of sect. *Hemiphyllanthus* have similar rusty pubescence and oblique leaf-bases, their flowers are very different.

39. Phyllanthus pulcher Wall. ex Muell. Arg. Linnaea 32: 49. 1863; DC. Prodr. 15(2): 421. 1866; J. J. Sm. Add. Cog. Fl. Arb. Jav. 12: 94–97. 1910. (PLATE XXIII, figs. A-B).

Diasperus pulcher ("Wall.") O. Ktze. Rev. Gen. 2: 600. 1891.

A small shrub c. 0.5–1.5 m. high; main stem slender, sparsely branched, c. 3–5 mm. thick, younger parts covered with reddish-brown dendritic hairs. Cataphylls persistent: stipules triangular-lanceolate, mostly 3–4 mm. long and 1.5–2 mm. broad, acuminate, basally dilated but scarcely auriculate, entire or obscurely denticulate, reddish-brown, scarious, hirsutulous at the base; blade lanceolate, often narrowly so, c. 3–4 mm. long. Decidu-

PLATE XXIII. FLOWERS AND LEAVES OF SUBG. Ericoccus and SUBG. Conami. Figs. A-B. Phyllanthus pulcher Wall. ex Muell. Arg. (Britton 1554 [GH]). Figs. C-F. Phyllanthus acuminatus Vahl (Baker 104 [GH]). Figs. G-J. Phyllanthus subglomeratus Poir. (Duss 2446 [GH]). Figs. K-L. Phyllanthus orbiculatus L. C. Rich. (Broadway 5564 [S]). (The androecia of P. acuminatus [fig. E] and P. subglomeratus [fig. I] are shown as removed to one side and seen from above).



WEBSTER, WEST INDIAN PHYLLANTHUS

ous branchlets steeply ascending, mostly 10–15 (–18) cm. long, 0.7–1 mm. thick, subterete, reddish-brown, hirsutulous as on the main stem, with c. 15–30 leaves; first internodes 5–10 mm. long, median internodes 5–7 mm. long. Leaves: stipules persistent, triangular-lanceolate, 2.5–4 mm. long and 0.9–1.2 mm. broad, acuminate, subentire, dark brown with lighter scarious margins. Petioles flattened, 0.8–1 mm. long. Leaf-blades membranous, glabrous, asymmetrically oblong to elliptic, mostly 18–28 mm. long and 8–14 mm. broad, abruptly pointed with a scarious tip, strongly inequilateral at the base (one side obtuse, the other acute); above olivaceous, sublucid, the slightly raised midrib and lateral veins not very conspicuous; beneath greyish, the midrib and laterals (c. 4–6 on a side) slightly raised, the laterals forming an irregular intramarginal loop with the reticulum of tertiary veinlets more or less conspicuous on both sides; margins plane, smooth, not thickened.

Monoecious; proximal axils of branchlet with cymules of several male flowers, the female flowers solitary in the distal axils; bracteoles conspicuously hirsutulous-ciliate.

Male flower: pedicel capillary (3-) 5–10 mm. long. Calyx-lobes 4 [rarely 5, ex Smith], decussate, subequal, triangular-ovate, c. 2.5–3 mm. long and 1.5–2 mm. broad, acuminate, conspicuously lacerate, the midrib sparsely branched or simple. Disk-segments 4, reniform or orbicular, thin and flat, smooth and entire, subpetaloid, c. 0.5–0.7 mm. broad. Stamens 2 [sometimes with the rudiment of a third, ex Smith]; filaments completely united into a very short column c. 0.1 mm. high, the anthers thus appearing sessile; connectives of anthers fused into a central knob; anthers 0.2–0.25 mm. long, 0.5–0.6 mm. broad; anther-sacs divergent, discrete (the androecium seemingly of 4 one-celled anthers), dehiscing horizontally; pollen grains spheroidal, reticulate, with a few scattered pores, c. 22–24 μ in diameter.

Female flower: pedicel 15–23 mm. long, capillary (slightly thickened above), subterete, smooth. Calyx-lobes 6, similar to those of the male but larger (to 3–3.5 mm. long) and the midrib regularly branched. Disk patelliform, with a thickened and fleshy somewhat pitted rim, enclosing the base of the ovary, becoming more or less split into discrete lobes. Ovary oblate, smooth, shallowly sulcate; styles free, spreading, alternating at the base with 3 erect blunt projections, bifid nearly to the base, the slender gradually tapered branches 0.3–0.4 mm. long.

Fruits not seen.

Flowering throughout the year, according to Smith.

Type: Malay Peninsula, Pulo-Penang, Wallich 7908 (G, HOLOTYPE).

DISTRIBUTION: native to Malaysia, introduced into the West Indies.

ST. VINCENT: old clearings, alt. 500 ft., H. H. & G. W. Smith 522 (NY). TRINIDAD: Port of Spain, Wall (S); Maracas, path to falls, Baker (TRIN 15037), Broadway 5459 (A, MO, S); Caura River valley, Britton 1554 (GH).

This exotic ornamental species is a relative newcomer to the West Indies,

having been first collected in St. Vincent in 1889 by the Smiths and in Trinidad in 1920 by Britton. Smith, who observed the plant in the living condition in Java, noted that it never produced any fruit; and Hooker (Fl. Br. Ind. 5: 302. 1887) also did not see any capsules. Evidently the plant spreads by vegetative means, perhaps by root-sprouts in the manner of *P. emblica* or *Breynia disticha*.

Among the West Indian species of *Phyllanthus*, *P. pulcher* is easily recognizable by the dark red lacerate calyx-lobes, the "cruciform" androecium of the male flower, and the dendritic trichomes on the axes.

Subgenus VI. Conami (Aubl.) Webster, Jour. Arnold Arb. 37: 345. 1956.

Conami Aubl. Hist. Pl. Guian. Fr. 926–927, pl. 354. 1775.

Herbs, shrubs, or trees with phyllanthoid branching, the branchlets pinnatiform or bipinnatiform. Monoecious or dioecious, cymules usually bisexual. Male flower: calyx-lobes 6; disk cupuliform or of discrete segments; stamens 3, filaments free or connate; anthers dehiscing more or less horizontally; pollen grains globose, echinulose, porate or brevicolpate. Female flower: calyx-lobes 6; disk cupuliform or of discrete segments; ovary of 3 carpels; styles more or less free. Fruit capsular; seeds smooth or verruculose.

The present interpretation of subg. Conami must be regarded as provisional, since it is based mainly on the few West Indian representatives and does not take into account the rather considerable number of South American species which may eventually prove to belong here. "Typical" members of sect. Nothoclema, which numerically predominate in the subgenus, are distinctive because of their bipinnatiform branchlets, echinulose pollen grains, and slenderly pedicellate flowers with hexamerous calyces. However, the type species of the subgenus, P. brasiliensis (Aubl.) Poir., has branchlets with very few lateral axes which approach the pinnatiform condition. There is still a very large gap between this species and P. orbiculatus of sect. Apolepis, but the latter has such similar pollen grains that there appears to be no alternative to considering it a reduced derivative of sect. Nothoclema.

KEY TO THE SECTIONS

Shrubs or trees with bipinnatiform branchlets; pollen grains brevicolporate; filaments united; seeds smooth.

13. Nothoclema

Herbs with pinnatiform branchlets; pollen grains porate; filaments free; seeds verruculose.

14. Apolepis

Sect. 13. Nothoclema Webster, Contr. Gray Herb. 176: 56. 1955.

Shrubs or trees with phyllanthoid branching; branchlets bipinnatiform, both ultimate and penultimate axes bearing leaves. Monoecious or dioecious; cymules with 1 or 2 female flowers and many males. Male flower: calyx-lobes 6; disk cupuliform or of 3 duplex segments: stamens 3, fila-

ments completely united into a short column; anthers dehiscing horizon-tally; pollen grains globose, echinulose (i.e., the exine with sculpturing of clavate projections), brevicolporate, the colpi each with two ora. Female flower: calyx-lobes 6; disk cupuliform, sometimes lobed; styles free, spreading, slender or dilated, bifid to lacerate. Capsule conspicuously veined; seeds plano-convex, essentially smooth (colliculose).

Type species: Phyllanthus acuminatus Vahl

Of the sections of *Phyllanthus* restricted to the New World, sect. *Nothoclema* is probably outstanding in the taxonomic difficulties which its representatives present. About 15 to 20 species have been proposed, but these are very poorly distinguished, and the identifications of South American specimens are almost wholly untrustworthy. Fortunately the two species in the West Indies are quite distinct and offer no problems in determination.

The origin and relationships of sect. Nothoclema are obscure; no other group, unless it possibly be the next section, appears to be at all closely related. Some affinity with sect. Elutanthos is suggested by general similarities in gross floral structure; but the species of that section differ strongly in their non-phyllanthoid branching and areolate pollen grains. Sect. Hemiphyllanthus includes some species which resemble sect. Nothoclema in having bipinnatiform branchlets, but they have areolate pollen grains and further differ in details of leaves, styles, and capsules. Similar floral structure is evident in sect. Ciccopsis, and although this group is obviously rather distant in affinity — as is indicated by its simply pinnatiform branchlets, free stamens, and tricolporate pollen grains — it possibly comes closer to representing the ancestral line to sect. Nothoclema than any other group in the West Indies.

The relationship of the following section, *Apolepis*, appears reasonably evident on the hypothesis that it is a reduced herbaceous derivative of sect. *Nothoclema*. The pollen grains of sect. *Apolepis* could be easily derived from those of *Nothoclema* by a simple reduction of the already short colpi to single pores. It must be granted, however, that in some characters, particularly the free disk-segments and stamens, sect. *Apolepis* is less specialized than sect. *Nothoclema*.

KEY TO THE WEST INDIAN SPECIES

Flowers borne mainly on ultimate axes of branchlet (the primary axis with 0-2 nodes bearing flowers, the distal nodes bearing only ultimate axes); leaf-blades ovate, abruptly cuspidate-acuminate; male flower with 3 reniform disk-segments; anthers acute; pedicel of female flower glabrous or scabridulous below.

40. P. acuminatus

Flowers borne at all nodes of both ultimate and primary axes of branchlet; leaf-blades elliptic, acute; male flower with cupuliform disk; anthers emarginate; pedicel of female flower hirsutulous.

41. P. subglomeratus

40. Phyllanthus acuminatus Vahl, Symb. 95. 1791; Muell. Arg. in

DC. Prodr. 15(2): 381. 1866; Fawc. & Rend. Fl. Jam. 4(2): 254. 1920. (PLATE XXIII, figs. C-F).

Phyllanthus conami Sw. Prodr. 28. 1788 (as to description, not as to type).

Diasperus acuminatus (Vahl) O. Ktze. Rev. Gen. 2: 598. 1891.

Conami conami (Sw.) Britton, Sci. Surv. Porto Rico 5(4): 475. 1924 (as to description).

Phyllanthus brasiliensis sensu Alain, Fl. Cub. 3: 52. 1953; not P. brasiliensis (Aubl.) Poir.

A slender rather sparsely branching shrub or small tree 2-8 m. high, the leafy branches with somewhat the aspect of fern-fronds. Older branches straight, subterete or bluntly angled, light brownish, the lenticels not conspicuous, mostly 3-5 mm. in diameter, the internodes c. 2-3.5 cm. long. New permanent branches not clustered at the apices of old branches but rather springing from the axils of deciduous branchlets of the previous year (and thus spaced 2-3.5 cm. apart), each producing during the season c. 3-6 deciduous branchlets. Cataphylls inconspicuous; stipules triangularlanceolate, c. 1.4-1.5 mm. long and 1.3 mm. broad, not auriculate at base, entire, pale and scarious; blade c. 1.3 mm. long and 0.7 mm. broad; blade and sometimes also the stipules deciduous, or the thickened bases persistent. Deciduous branchlets bipinnatiform (except for the first branchlet of a new branch, which is usually simply pinnatiform); primary axis (15-) 20-50 cm. long, (1-) 2-3 mm. broad, green, smooth on the ventral (upper) side but usually scabridulous or hirsutulous dorsally, more or less tetragonous, the dorsal and ventral angles blunt but the lateral angles sharply winged and dilated just below the nodes; nodes of primary axis (5-) 9-18 (-21), first internode mostly 2-5 cm. long, distal internodes (1-) 1.5-3 cm. long. Ultimate axes leafy and floriferous, similar to the primary axis in form and texture but more flattened, (5-) 7-20 cm. long, with (5-) 7-15 (-22) leaves; first internode 1.2-3 cm. long, distal internodes (0.5-) 1-2.5 cm. long. Leaves on both primary and ultimate axes similar but averaging somewhat larger on the primary: stipules triangular-lanceolate, blunt, not auriculate, entire, more or less persistent and becoming thickened and scarious (though often the tip deciduous), sometimes reflexed, those of the primary axis up to c. 1.3 mm. long and 1.1 mm. broad, those of the ultimate axes c. 0.7-1 mm. long and 0.4-0.7 mm. broad (or sometimes about as large as those of the primary axis). Petioles flattened and densely scabridulous or hirsutulous adaxially, convex and nearly smooth abaxially, 1.5-3 mm. long. Leaf-blades membranous to chartaceous, ovate or elliptic (sometimes very broadly so), (1.5-) 2.2-4.5 cm. long, (0.7-) 1.2-2.5 cm. broad, rather abruptly and bluntly cuspidate-acuminate at the tip, usually obtuse at the base; above olivaceous, lucid as though varnished (under a bright light), more or less scabridulous-roughened (often conspicuously so on the midrib), the midrib raised proximally but obscure toward the tip, the laterals (c. 5 or 6 on a side) only slightly raised; beneath pale and greyish, smooth except for the veins, the midrib prominently raised and running to the tip, the laterals also raised, connecting with the tertiaries to form an irregular reticulum; margins scarcely thickened, definitely roughened, plane.

Monoecious; primary axis producing flowers at the 1 or 2 proximal nodes but not at the subsequent nodes with ultimate axes (and thus entirely non-floriferous when the first node occasionally bears an ultimate axis) except for the simple branchlet at the beginning of the year's growth; this latter, and the ultimate axes, usually floriferous at every node. Flowers in contracted bisexual cymules, the peduncle becoming up to 1 mm. long, the female flower central and solitary (rarely accompanied by a second), the male flowers lateral, usually 6–20.

Male flower: pedicel capillary, smooth, 3–4.5 mm. long. Calyx-lobes 6, biseriate, 1-nerved, with green midrib and broad whitish hyaline margins; outer lobes narrowly oblong, slightly carinate dorsally, the acutish tip slightly inflexed, c. 0.9–1 mm. long and 0.4–0.6 mm. broad; inner lobes obovate (almost flabellate), flaring outwards from about the middle, c. 0.9–1.2 mm. long and broad. Disk-segments 3, massive, subcubical with a deep adaxial channel (and thus more or less reniform), glandular-pitted but smooth in outline, c. 0.3–0.35 mm. broad. Stamens 3, filaments completely united into a short column c. 0.15–0.3 mm. high; anthers triangular-ovate, acutish, usually minutely apiculate, flattened, sessile atop the column, the bases contiguous and the common connective thus more or less triangular, c. 0.3–0.4 mm. long and broad; anther-sacs contiguous but not confluent across the tip, dehiscing horizontally; pollen grains globose, somewhat angular, with 3 short diorate colpi, c. 19–20 μ in diameter.

Female flower: pedicel (5–), 7–12 mm, long [in West Indian populations], slender, obscurely to conspicuously angled, scabridulous (sometimes smooth above) but not hirsutulous. Calyx-lobes 6, biseriate, 1-nerved, greenish-herbaceous with rather narrow scarious whitish entire margins, never hirsutulous dorsally; outer lobes elliptic or triangular-elliptic, c. 1.1–1.4 mm, long and 0.5–0.9 mm, broad; inner lobes broadly ovate, c. 1.5–1.7 mm, long and 1–1.13 mm, broad. Disk cupuliform, massive, more or less 3-lobed (as though formed of 3 reniform segments as in the male), inconspicuously pitted, the rim minutely crenulate. Ovary oblate, trigonous, deeply sulcate between the locules. Styles free, flattened, appressed and spreading (the tips sometimes upcurving), 0.4–0.6 mm, long, divided ¼ to ½ their length; style-branches subterete or flattened, subparallel, sometimes dilated and again lobed.

Capsule oblate, olivaceous, rather conspicuously veiny, 4.5–5 mm. in diameter. Columella massive, conical, c. 2 mm. long. Seeds plano-convex, often coherent in pairs, (2.2–) 2.5–2.8 mm. long, (1.7–) 1.8–2 mm. broad, reddish-brown, sometimes mottled, smooth with a honeycomb pattern imparted by the epidermal cells; hilum elliptic, c. 0.5–0.6 mm. long; micropylar end sometimes with rudimentary elliptic corneous caruncular swellings.

Collected in flower [in West Indies] May through November, in fruit July through December.

Type: Trinidad, Ryan (C, HOLOTYPE).

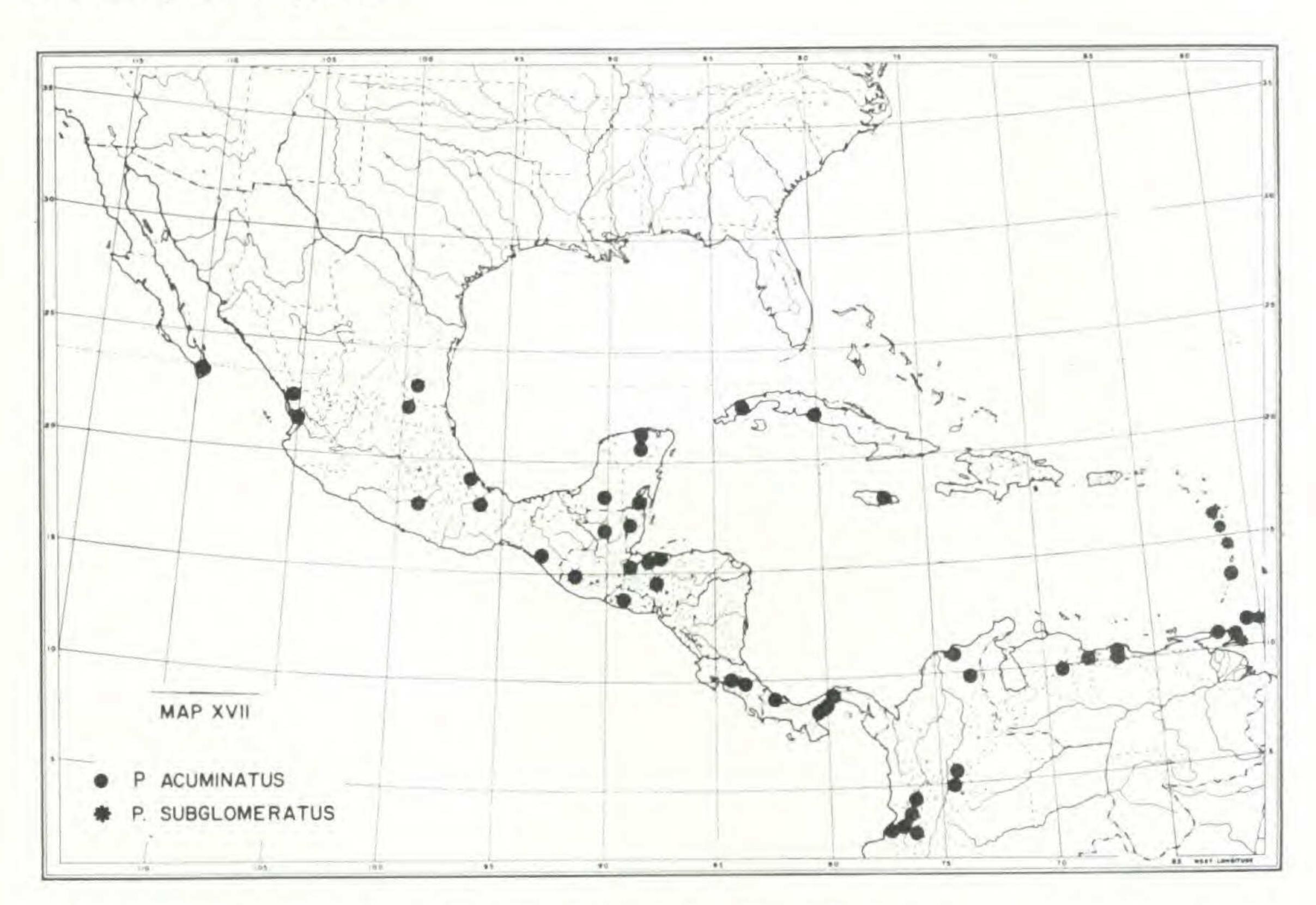
Distribution: widespread from northern Mexico (Tamaulipas) south

to northern Argentina (Jujuy, Salta), Paraguay, and central Brazil (Minas Geraes); range discontinuous in the West Indies (MAP XVII).

CUBA. Pinar del Río: Pinar del Río City, in thickets at Laguna Gauyabo, Ekman 18245 (S); Baños San Vicente, Britton, Britton, & Gager 7487 (NY); Viñales, near Pan de Azúcar, Alain 4435 (GH); Viñales, Palmarito, in thickets at a brook, Ekman 16624 (S); San Diego de los Baños, in pinelands, at a brook, Ekman 17769 (S); San Diego, Van Hermann 3219 (NY). Habana: Santiago de las Vegas [cult.], Baker 104 (C, NY, P). Las VILLAS: Trinidad Mountains, scrubby woods near the top of Pico Sombrero, Webster 4769 (GH).

JAMAICA. St. Mary: near Castleton, Harris 8409 (F, JAM, NY); Wag Water Valley, near Castleton, Harris 11147 (F, JAM, NY, US).

LESSER ANTILLES. St. Vincent: 1816, Caley (G, P). Tobago: Easterfield, Broadway 4555 (C, L, MO). Trinidad: Ryan (C); thicket, Port-of-Spain, Britton 990 (GH); ad Caroni flumen, in sylvestribus, Eggers 1428 (C); Arima, in sylvis, Eggers 1184 (P, W); Laventille, D. W. Alexander (TRIN 4378, 4555); savannah, road to Lambie, Finlay (TRIN 2464); Santa Cruz, among cocoa, Broadway 2659 (MO).



Map XVII. Caribbean distribution of the West Indian representatives of sect. Nothoclema.

Phyllanthus acuminatus, in contrast to most of the other taxa in sect. Nothoclema, is a clearly circumscribed species and is as readily indentifiable as it is widely distributed. Its characteristic leaves with roughened upper surface and abruptly narrowed tip, male disk of 3 segments, and non-hirsutulous female pedicel together make its recognition easy. Furthermore, it appears to be exceptional in that it is never used as a fish-poison in the manner of the majority of species of sect. Nothoclema. The prevalent con-

fusion (in herbaria and in the literature) of *P. acuminatus* with *P. brasiliensis* may ultimately be attributed to the misconception of Swartz, who mistakenly assumed the Jamaican representative of sect. *Nothoclema* to be conspecific with Aublet's *Conami brasiliensis* and proposed the name *Phyllanthus conami* to include both plants. This proposal of the new epithet *conami* is of course illegitimate under the present rules, since Aublet's type was included in Swartz's specific concept; consequently, the combination *P. brasiliensis* (Aubl.) Poir. has been applied by various authors to the species here called *P. acuminatus*. However, there is no doubt that the plant described by Aublet is quite distinct from *P. acuminatus* and in fact is much more closely related to the other West Indian member of the section, *P. subglomeratus*. In contrast to *P. acuminatus*, *P. brasiliensis* does not occur outside of South America.

The spotty distribution of *P. acuminatus* in the West Indies is striking, for its geographical pattern is not duplicated by any other species. The plant does not appear to be particularly common anywhere in the West Indies (except possibly in Trinidad) and in Jamaica and Cuba is comparatively rare and local. This sporadic occurrence, and the fact that there is no evident morphological variation among the various insular populations, make it appear likely that the range of *P. acuminatus* within the West Indies is the result of relatively recent dispersal. The absence of the species from the central Caribbean, especially Hispaniola and Puerto Rico, can perhaps be best explained on the assumption that it has invaded the West Indies from two separate points, Cuba and Jamaica being colonized from Central America and Trinidad and Tobago from northeastern South America.

41. Phyllanthus subglomeratus Poir. Encycl. Method. 5: 304. 1805 (as P. subglomerata). (PLATE XXIII, figs. G-J).

Phyllanthus brasiliensis β oblongifolius Muell. Arg. Linnaea 32: 27. 1863; DC. Prodr. 15(2): 383. 1866.

Phyllanthus conami sensu Duss, Fl. Phan. Ant. Fr. 22. 1896; non Sw.

A shrub or small tree 2–4 m. high, with the habit of *P. acuminatus*, the main branches often tortuous and knotted (Duss). Branches subterete, sparsely hirtellous but becoming smooth with age; branchlets probably borne in the manner of *P. acuminatus*, but apparently all bipinnatiform. Cataphylls of permanent branches becoming thickened and persistent: stipules broadly ovate-triangular, c. 1.7–2 mm. long and broad, bluntly pointed, more or less auriculate at the base, entire, dark reddish-brown in the center and scarious at tip and margins, persistent; cataphyll blade c. 1.3 mm. long, deciduous. Deciduous branchlets apparently always bipinnatiform with both flowers and ultimate axes produced at all the nodes of the primary axis. Primary axis 15–40 cm. long, c. 1.8–3.5 mm. thick, drying brownish, ventrally smooth and dorsally hirsutulous as in *P. acuminatus*, proximally more or less terete, becoming tetragonous distally but not sharply wing-angled, with c. 10–25 nodes; first internode mostly (15–) 20–40 mm. long, distal internodes (10–) 15–25 (–30) mm. long. Ultimate

axes floriferous and leafy precisely as the primary axis but more flattened, 7-16 cm. long, with c. 15-25 leaves; first internode mostly 5-10 (-13) mm. long, distal internodes (2-) 4-9 mm. long. Leaves similar on both primary and ultimate axes: stipules triangular-lanceolate, bluntly acute or acuminate, subauriculate, entire, dark and thickened at the base, paler and scarious at tip and margins, more or less persistent, those of the primary axis c. 1.3-1.7 mm. long and nearly as broad, those of the ultimate axes 1-1.4 mm. long, 0.7-1.1 mm. broad. Petiole flattened and densely hirsutulous adaxially, convex and nearly smooth abaxially, 1.2-1.5 mm. long. Leaf-blade membranous, elliptic, (12-) 14-26 mm. long, (5-) 6-9 (-11) mm. broad, gradually narrowing to an acute tip (this sometimes slightly constricted but never attenuate), cuneate at the base; above olivaceous, rather dull, never appearing varnished under a bright light, smooth and glabrous (the midrib excepted), midrib slightly raised and hirsutulous proximally, smooth and becoming obscure toward the tip, laterals (3-5 on a side) smooth, not conspicuous; beneath paler, smooth, the midrib rather prominently raised, slightly hirsutulous proximally, running to the tip, the laterals and tertiaries forming a fine reticulum; margins smooth, plane, unthickened.

Monoecious; flowers produced only on deciduous branchlets; primary axis producing flowers at all the nodes, including those bearing ultimate axes (sometimes a few proximal axils barren?). Flowers in contracted bisexual cymules, the peduncle becoming c. 0.5–0.7 mm. long; female flower central and solitary, male flowers lateral and numerous.

Male flower: Pedicel capillary, smooth, mostly 5–6 mm. long. Calyx-lobes 6, rather unequal but the inner series not sharply different from the outer, triangular, 0.8–1 mm. long, 0.5–0.7 mm. broad, obtuse or subacute, 1-nerved, with greenish herbaceous area around midrib (brownish in dried specimens) and narrow hyaline scarious entire margins. Disk a shallow cup with a rather narrow subentire rim, not evidently glandular, c. 0.8 mm. across. Stamens 3; filaments united into a very short column c. 0.15 mm. high, the discrete anthers thus appearing nearly sessile on the receptacle; anthers with constricted connectives, emarginate, not flattened, c. 0.2–0.25 mm. long and 0.3–0.35 mm. broad; anther-sacs subglobose, dehiscing horizontally, the slits completely confluent. Pollen grains globose, echinulose as in *P. acuminatus* but the germ-pores obscure, c. 19–22 μ in diameter.

Female flower: Pedicel [in flower] c. 1.5 mm. long, terete below, becoming angled above, hirsutulous the entire length. Calyx-lobes 6, biseriate but about equal in size, triangular-lanceolate, 1–1.2 mm. long and 0.7–0.8 mm. broad, bluntly pointed, 1-nerved with an herbaceous mid-area and narrow scarious minutely denticulate margins. Disk cupuliform, 6-angled, covering less than ½ the height of the ovary, glandular-pitted, the rim minutely crenulate. Ovary subglobose, smooth, sessile, not angled or deeply sulcate. Styles free, spreading or commonly more or less ascending, c. 0.3–0.35 mm. long, divided ½ to ¾ their length; style-branches more or less divergent but not recurved, tapering to blunt tips.

Fruit not seen; apparently never produced by West Indian plants. Flowering throughout the year.

Type: Martinique, Herb. Lamarck (P, HOLOTYPE).

DISTRIBUTION: probably native to South America, but exact range and origin not yet determined (MAP XVII).

LESSER ANTILLES. GUADELOUPE: Matouba, Duss 212 (P), 2446 (GH, MO, US); Grande Terre, L'Herminier (A, P); haies, St. Claude, R. P. Quentin 527 (P); chemin de la Regrettée, Trois-Rivières, R. P. Quentin 671 (P); chemin de la Soufrière, St. Claude, subspontané, Stehlé 63 (A). Dominica: in fruticetis ad Grande Bay, Eggers 662 (GH, GOET, L, W); Imray s.n. (GOET), 97 (GH). Martinique: St. Pierre, Belanger 294 (G, P), 283, 832 (P); Ajoupa-Bouillon, Marin, &c., Duss 2047 (NY); Hahn 322 (G, GH, L, P, W); Mouret 109 (P); Plée (P); Herb. Richard (P); Ryan (C); Sieber Fl. Martin. 223 (GH, GOET, L, MO, W). Tobago: Valencia road, roadside, Baker (TRIN 14864). Trinidad: Ryan (C).

Although *P. subglomeratus* is thus far known only from the Lesser Antilles (including Trinidad), it cannot with any confidence be classed as a species endemic to this region. Several collectors have noted that the plant occurs both cultivated and in a semi-wild state, and Plée has described (in the notes accompanying his specimens in the Paris Museum) the utilization of the plant for fishing in Martinique in 1820: dams were thrown across streams to form pools and the leafy branches of *P. subglomeratus* were simply tossed into the water; in a few minutes the larger fish were stunned so that they could be easily caught, while the smaller ones were killed. The common native usage of the plant, and the circumstance that not a single fruit is present on any of the specimens, strongly suggests that the present distribution of *P. subglomeratus* in the Lesser Antilles is largely affected by the activities of man.

The status of P. subglomeratus has been confused since its publication, probably because Poiret cited P. acuminatus Vahl, with a question mark, as a synonym of his new species. It might be argued that P. subglomeratus is therefore only a superfluous name for P. acuminatus, but the manner in which Poiret cited the latter suggests rather that he was merely raising the possibility that Vahl's species was the same as his, and he definitely did not refer to any plant except the type specimen from Martinique. Mueller, perhaps influenced by Poiret's citation, incorrectly referred P. subglomeratus to the synonymy of P. acuminatus but at the same time listed specimens of the former (collected on Martinique by Plée and Sieber) under his P. brasiliensis var. oblongifolius. Mueller's interpretation of these collections as representing a variety of the South American P. brasiliensis is not unreasonable, for these two plants are undoubtedly closely related. The latter, originally named Conami brasiliensis by Aublet, was based on a cultivated shrub observed by Aublet in French Guiana, but said by the natives to have been introduced from Pará in Brazil. This plant too was used in stunning fish and, in fact, "Conami" according to Aublet was an aboriginal generic name for fish-poisoning plants. However, while the

plant observed by Aublet is doubtless a near relative of *P. subglomeratus*, it differs in its more sparsely ramified (sometimes simple) branchlets, broadly ovate leaves, and hirsutulous ovary. It is conceivable that *P. subglomeratus* may represent a clone derived from some aberrant population of *P. brasiliensis* (or from one of the several closely related species), but for the time being the definite morphological features of the Antillean plant would appear to justify maintaining it at specific rank.

Further investigations of P. subglomeratus might be of ethnobotanical interest, since it seems probable that the plant was introduced into the Antilles by the Carib Indians and its history may be connected with the migrations of these tribes.

Sect. 14. Apolepis, sect. nov. 18

Herbs with phyllanthoid branching, the branchlets pinnatiform. Monoecious; cymules bisexual. Male flower: calyx-lobes 6; disk-segments 6; stamens 3, filaments free; anthers emarginate, dehiscing horizontally; pollen grains globose, echinulose, porate. Female flower: calyx-lobes 6; disk-segments 6; styles free, bifid. Capsule not veiny; seeds verruculose.

Type species: Phyllanthus orbiculatus L. C. Rich.

It is with some reluctance that another monotypic section is described within a genus that is already overburdened with them; but although P. orbiculatus superficially resembles members of sect. Phyllanthus, its pollen grains are so different that it cannot be closely related. On the other hand, its bisexual cymules and slenderly pedicellate flowers, as well as its pollen grains, show such a resemblance to those of sect. Nothoclema that P. orbiculatus seems best placed in subg. Conami rather than in subg. Phyllanthus. However, the simply pinnatiform branchlets, herbaceous habit, and free stamens of P. orbiculatus are so discordant with the characters of sect. Nothoclema that it would seem preferable to create a new section rather than to modify unduly the limits of sect. Nothoclema.

42. Phyllanthus orbiculatus L. C. Rich. Act. Soc. Hist. Nat. Paris 1: 113. 1792. (PLATE XXIII, figs. K-L).

Phyllanthus nummulariaefolia Poir. Encycl. Method 5:302. 1804 (as to Guiana collection, not as to type).

Phyllanthus poiretianus Muell. Arg. Linnaea 32: 39. 1863.

Phyllanthus orbiculatus a genuinus Muell. Arg. in DC. Prodr. 15(2): 401. 1866.

Diasperus orbiculatus (Rich. "emend.") O. Ktze. Rev. Gen. 2: 600. 1891.

Annual herb c. 1-5 dm. high, main stem c. 0.5-1.5 mm. thick, un-

¹⁸ Sect. Apolepis, sect. nov. Herbae monoicae, ramificatione more sectionis *Phyllanthi*, ramulis simpliciter pinnatiformibus, cymulis bisexualibus; flore masculo lobis calycis 6, staminibus 3, filamentis liberis, antheris plusminusve horizontaliter dehiscentibus, granis pollinis globosis echinulosis; flore femineo laciniis calycis 6, segmentis disci 6, stylis liberis bifidis; capsula non venosa, seminibus verruculosis. — Species typica *Phyllanthus orbiculatus* L. C. Rich.

branched or sparsely branched, brownish, terete, smooth; internodes c. 0.3-2 cm. long. Cataphylls: stipules oblong-lanceolate, (0.5-) 0.7-0.9 mm. long, 0.25-0.35 mm. broad, acute (often abruptly so) at the tip, truncate at the base, entire or sometimes with one or two teeth near the apex, reddish-brown, scarious; blade linear, 0.6-0.9 mm. long, 0.1-0.15 mm. broad, sometimes fused with the stipules in the lower third. Deciduous branchlets (3-) 5-10 (-12) cm. long, c. 0.15-0.25 mm. thick, olivaceous, smooth, subterete, with (7-) 9-20 (-25) leaves, often somewhat zigzag; first internode (6-) 9-13 (-16) mm. long, median internodes mostly 2-5 mm. long. Leaves: stipules ovate, 0.4-0.7 mm. long, 0.2-0.3 mm. broad, acute or acuminate, entire, reddish with indistinct yellowish margins, scarious. Petioles 0.3-0.6 mm. long. Leaf-blades membranous to chartaceous, orbicular or broader than long, mostly 5-10 mm. long and about as broad, broadly obtuse and usually apiculate at the tip, obtuse at the base; above olivaceous, smooth or minutely wrinkled, the midrib evident but not raised, the laterals obscure; beneath pale, more or less greyish, the midrib salient and running to the tip, the laterals (c. 3 or 4 on a side) slightly raised, the tertiary veinlets evident or obscure; margins plane, scarcely thickened, smooth or obscurely roughened.

Monoecious; cymules bisexual, of a single female and 1 or 2 male flowers.

Male flower: pedicel capillary, becoming mostly 2.5–4 mm. long. Calyx-lobes 6, elliptic-oblong, c. 0.6–0.8 mm. long and 0.3–0.4 mm. broad, narrowed to an acute tip, entire, thin and subhyaline, the midrib unbranched. Disk-segments 6, subentire, more or less concave, only 0.1–0.15 mm. across. Stamens 3, filaments free; anthers c. 0.15–0.2 mm. long, 0.3 mm. broad, emarginate between the discrete anther-sacs, dehiscing horizontally; pollen grains nearly spherical, echinulose, porate, c. 16–17 μ in diameter.

Female flower: pedicel becoming c. 2.5–3 mm. long, terete, olivaceous, minutely scabridulous below. Calyx-lobes 6, linear-oblong, 0.7–0.8 mm. long, 0.25–0.3 mm. broad, acute, entire, olivaceous with yellowish scarious margins, the midrib unbranched. Disk dissected into 6 discrete segments, these elliptic-oblong to obovate, entire, rather thin, c. 0.2 mm. long. Ovary deeply sulcate, smooth; styles free except at the very base, spreading and appressed to the top of the ovary, c. 0.15–0.2 mm. long, divided c. ½ their length, the branches circinately recurving, the slender tips curled inwards.

Capsule trigonous, smooth, c. 2.5 mm. in diameter, stramineous, not veiny. Columella slender, c. 0.75–0.8 mm. long. Seeds trigonous, becoming fuscous, c. 1.1–1.25 mm. long, 1–1.1 mm. radially and tangentially, verruculose with more or less transversely elongated dots arranged in irregular longitudinal rows on the back and sides.

Type: French Guiana, Cayenne, Leblond (P, HOLOTYPE; C, ISOTYPE).

DISTRIBUTION: widespread in South America from Bolivia and Paraguay north to Colombia and Venezuela, reaching its northeastern limit in Trinidad.

TRINIDAD: San Juan, roadside, *Broadway 5564* (S), stony grassy lands, 1928, *Broadway* (MO, S); Cedros, prospect near the lagoon, *Broadway* (TRIN 8540); Icacos, *Broadway* (TRIN 7404, 8539); Icacos, near the sea, sandy land, St. Quinton, *Broadway 7833* (MO).

Phyllanthus orbiculatus appears to be a taxonomically isolated species, the relationships of which need to be further investigated. Although it has the general aspect of species of sect. Phyllanthus, it stands out even superficially by its elongated pedicels and broad leaves and, of course, it differs esentially in its inflorescence and pollen grains. Mueller (DC. Prodr. 15[2]: 401. 1866) placed it between P. subemarginatus and P. claussenii in the group of sect. Euphyllanthus having widely separated anther-sacs. However, the anthers of P. claussenii are very different from those of P. orbiculatus in that the anther-sacs are much more widely separated and completely discrete as though the filament terminated in two one-celled anthers, whereas the anthers of P. orbiculatus are merely deeply emarginate. Furthermore, the pollen grains of P. claussenii and its Brazilian relatives are more or less typical of those in sect. Phyllanthus and appear very different from those of P. orbiculatus.

It is rather curious that none of the older collectors encountered *P. orbiculatus* in Trinidad, the earliest record apparently being the collection made at Icacos in 1915 by Broadway (TRIN 7404). This suggests that the species is either a newcomer to the island or at least has been extending its range in recent times.

(To be continued)